THE ECOLOGY OF BIRDS IN THE URBAN LANDSCAPE: AVIAN COMMUNITY COMPOSITION, DISPERSAL, AND SURVIVAL ACROSS THE RURAL-TO-URBAN GRADIENT IN WASHINGTON D.C.

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ABSTRACT

Brian Spence Evans: The Ecology Of Birds In The Urban Landscape: Avian Community Composition, Dispersal, And Survival Across The Rural-To-Urban Gradient In Washington D.C. (Under the direction of Allen H. Hurlbert and Peter P. Marra)

Urbanization during the latter half of the twentieth century has altered habitats, restructured wildlife communities, and influenced the range sizes and population dynamics of animal species. While many bird species persist in urban environments, little is known about the consequence of urbanization on birds – in part because urban landscapes confer conflicting pressures, such as exposure to novel predators, and benefits, such as anthropogenic food resources. Here, we explore the influence of urbanization on birds in the Washington D.C. metropolitan area using a unique study design that addresses the community composition, dispersal behavior, and survival of birds across the rural-to-urban gradient within the context of a regional citizen science project. We found supportive evidence for environmental filtering of bird communities by assessing variation in functional diversity as well as the proportional and apparent abundance of avian life history guilds within sites across the rural-to-urban gradient. To address the influence of urbanization on avian dispersal, we explored the degree of permeability of habitats in association with the spatial distribution of four species of birds banded and reencountered in subsequent years. There was supportive evidence that, for two of the four species, the distribution of habitat influences settlement patterns of birds and thus shapes dispersal behavior in human-dominated landscapes.

Finally, we used mark-recapture data to assess variation in adult survival across the rural-to-urban gradient to test hypotheses about the processes by which urbanization is expected to influence avian survival. Adult survival was enhanced in suburban and urban habitats for four of our seven focal species and there was no evidence in support of an influence of urban land cover on survival for the remaining species. Taken cumulatively, this research addresses three distinct ecological relationships between birds and their environments and provides a significant advancement in our understanding of the influence of urbanization on wildlife populations.

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LIST OF ABBREVIATIONS AND SYMBOLS

AIC_C	Akaike's Information Criteria, adjusted for a small sample size
BCI	Body condition index
CAN	Canopy cover
CI	Confidence interval
FD	Functional diversity
IMP	Impervious surface
NN	Neighborhood Nestwatch
SES	Standardized effect size
β	Beta parameter estimate
Φ	Apparent survival estimate

CHAPTER 1: ENVIRONMENTAL FILTERING OF AVIAN COMMUNITIES ALONG A RURAL-TO-URBAN GRADIENT IN GREATER WASHINGTON D.C.

Introduction

The impact of urbanization on biological communities has become a subject of key conservation concern in the 21st century. While urban environments make up just 5.6 percent of the land cover (US Census Bureau 2012), the shift from rural to urban land use is considered to be the second leading cause of species endangerment and extinction in the United States (Czech and Krausman 1997). Under current rates of urban expansion, developed land in the United States is projected to increase by 63% from 2001 to 2051. This increase is expected to drive a loss of more than 10% of habitat for one-third of the bird species currently at risk of extinction (Lawler et al. 2014) and thus urbanization is expected to become the most important driver of species extinction over this century (Marzluff 2001). Considering the rapid expansion of urban environments, mitigating the projected loss in biodiversity is partially dependent on understanding how urbanization structures biological communities and the subsequent development of wildlife management strategies that incorporate urban ecosystems (Miller and Hobbs 2001).

As landscapes become urbanized, avian communities are impacted by modification to the structure and composition of habitats within the suburban and urban matrices (Beissinger and Osborne 1982, Marzluff et al. 1998). Characteristic changes associated with urbanization include an increase in non-native plant species cover (e.g., White et al. 2005), decline in the structural diversity of vegetation (e.g., Gavareski 1976; Evans et al. 2009), and a decrease in habitat availability for native species (Marzluff 2001). Because species are known to have a differential response to human-built

environments, communities that occupy urban environments are often distinct from those that inhabit areas of lower human impact and tend to be dominated by higher densities of a few species able to persist in these habitats (e.g., Chace and Walsh 2006; McKinney 2006; Kark et al. 2007; Conole and Kirkpatrick 2011).

Patterns in avian community structure along the rural-to-urban gradient are thought to be determined largely by an interaction between land use and life history traits of associated species that determine whether a given species will be a "winner" (urban-adapted or urban-exploiter species) or "loser" in human-dominated landscapes (urban-avoiding species; McKinney and Lockwood 1999; Blair 2001). Species with specialist niche requirements are expected to be especially sensitive to human-induced habitat modification and may therefore experience high rates of local extinction across the urban habitat matrix (Devictor et al. 2007). For example, obligate insectivores (Lancaster and Rees 1979) and cavity nesting species (Blewett and Marzluff 2005) may be considerably impacted by even minor modifications of the urban landscape, while species with omnivorous or generalist nesting habits are expected to be positive affected by, or even thrive, in urban environments (reviewed in McKinney and Lockwood 1999). It is thus hypothesized that urban bird communities will exhibit "biotic homogenization" by which urban communities across biogeographic regions will be more taxonomically and functionally similar than their rural counterparts due to differential resource opportunities across life history traits (McKinney and Lockwood 1999; Devictor et al. 2007; Luck and Smallbone 2011). The effects of urbanization on local and regional habitat structure and function are therefore expected to act as an environmental "filter" on avian communities by excluding species with specialist traits that are maladapted to urban habitats while providing additional habitat for species with traits, such as omnivorous diets, that may facilitate their persistence in these environments (Croci et al. 2008; Jokimaki et al. 2014). As the strength of environmental filtering increases across the urbanization gradient, both species richness

and functional diversity – the variation in life history traits associated with local communities – are expected to decline with increasing urbanization (e.g., Ortega-Alvarez and MacGregor-Fors 2009; Sol et al. 2014). While such declines are consistent with environmental filtering, species richness might vary along spatial gradients for other reasons (e.g., resource availability). Because any trend in richness could generate a parallel trend in functional diversity through a simple sampling effect, environmental filtering can only be inferred when using a metric of functional diversity that takes species richness into account (Petchey et al. 2007; Flynn et al. 2009).

A decline in species richness, and often an increase in abundance, across the rural-to-urban gradient has been a widely observed phenomenon across biogeographic regions (e.g., Jokimaki and Suhonen 1993; Clergeau et al. 1998; McKinney 2006), however, whether urbanization acts as an environmental filter on avian communities remains largely unclear. Although numerous studies have addressed avian community composition at varying intensities of urbanization (e.g., Lancaster and Rees 1979; Blair 1996; Crooks et al. 2004), comparably few studies have addressed the response of guilds to urbanization across the continuous rural-to-urban gradient (but see Crooks et al. 2004; Blair and Johnson 2008; Garaffa et al. 2009). Moreover, the associations between life history guilds and habitat characteristics may vary widely among biogeographic regions (Hansen and Urban 2002), thus guild-specific measures of environmental filtering in response to urbanization have often produced conflicting results (Evans et al. 2011). Attributing the response of individual guilds to environmental conditions are also confounded by joint membership of species across guilds, thus the response of a guild to urbanization necessitates accounting for the correlation structure between guilds across multiple niche axes (Croci et al. 2008).

As a decline in species richness does not describe whether affected species are removed from the local species pool as a function of life history traits, and the response of individual guilds

vary by region and are confounded by collinearity, neither measure provide clear evidence for the filtering effect of urbanization. Functional diversity provides a metric of environmental filtering (e.g., among plant communities, see Coyle et al. 2014) that is insensitive to the response of individual guilds to urbanization and that can therefore can be broadly applied across regions despite conflicting responses among life history guilds. While previous research has suggested that urban bird communities are filtered as a function of avian life history traits (notably Croci et al. 2008), no previous study has yet tested for environmental filtering by assessing the influence of urban land cover on the functional diversity of bird communities.

Here, we evaluate the composition of bird communities at sampling locations spanning the rural-to-urban gradient in the Greater Washington D.C. to assess whether urban habitats act as an environmental filter on avian communities. We use thee distinct lines of evidence to test and explore the nature of environmental filtering within our study region, testing the following predictions: 1) Species richness declines with increasing urban land cover; 2) Functional diversity, as expressed by the diversity of life history guilds, declines with increasing urban land cover, independent of species richness; 3) Species with life history traits associated with specialist dietary habits (e.g., insectivores), foraging behaviors (e.g., foliage-gleaners), nesting habits (e.g., cavity nesters), and long-distant migration are more sensitive to urban land cover than other species within the regional species pool (see Fig 1.1 for guild-level predictions). We examine the response of individual guilds to urban land cover by assessing variation in the estimated abundance (i.e., abundance accounting for detection) and relative abundance. These metrics, when used in tandem, provide a measure of both how a guild responds relative other guilds for a given trait (relative abundance) and whether urban land cover positively or negatively influences avian abundances for that guild. Furthermore, because the attribution of a guild response is likely confounded by co-membership between guilds, we asses we assess the degree of correlation between guilds. The use of three distinct lines of evidence and

addressing the abundance, relative abundance, and collinearity between guilds provides a robust and novel analysis of both the extent and nature of environmental filtering in urban habitats.

Methods

Avian count data were collected as a part of the Neighborhood Nestwatch Program (NN), a citizen science project run by the Smithsonian Migratory Bird Center. NN has established a network of sampling sites within the Greater Washington D.C. metropolitan area with sampling predominantly located at the homes of project participants. Project participants are accepted into the study based on a wide range of criteria, including level of interest, expected degree of engagement, and position along the rural-to-urban gradient, as assessed by the proportion of impervious surface relative to the impervious surface within our study region and that of existing sites. Habitats represented by study sites range from rural open and forested areas, to suburban and urban environments. In order to more accurately characterize the rural-to-urban gradient within our study region, supplemental survey data were collected from an additional 30 randomly sampled sites (total sites = 203) from forested and core urban (> 50% impervious surface) habitats, habitat classes which were under-represented within the NN study (see Evans et al. 2015, Appendix A). Random sampling points were jittered to the nearest accessible location.

Between the years of 2009 and 2012, technicians visited sites once annually during avian breeding season (May-August) and conducted a ten minute, fixed radius point count (50 m, Petit et al. 1995) between the hours of 0700 and 1000 local time. The distances between the observer and individual birds were estimated in 10 m distance segments (e.g., 0-10 m). Flyovers were not recorded as they may not be representative of birds with established territories within the point count radius. Likewise, count data were restricted to species with known breeding ranges within our study region. Because the number of years a given site was visited was variable (between one and three years), one

point count was sampled randomly from a given site for analysis. For each species observed, we evaluated guild representation across dietary, foraging, migratory, and nesting guilds (Table 1.1), obtained from the avian trait database compiled by Wilman et al. (2014) and supplemented when necessary with avian life history information from the Birds of North America (Rodewald et al. 2015).

We used the proportion of impervious surface to characterize the degree of urbanization of each site. While we acknowledge the proportion of impervious surface is just one component that can be used to approximate urban intensity, this proxy variable has been found to be predictive of avian demographic response to urbanization (see Ryder et al. 2010, Evans et al. 2015) and adequately reflects the variation in habitat distribution and quality across the rural-to-urban gradient (reviewed in McKinney 2002). Across our samples, impervious surface was highly predictive of core urban and suburban land cover types with sites at the rural end of the urbanization gradient predominantly comprised of agricultural or forested habitats (see Evans et. al 2015, Appendix A). We used the *raster* package in R (Hijmans 2014) to calculate the proportion of impervious surface (30 m resolution, Xian et al. 2011) within a 100 m neighborhood of each sampling location. Though the scale at which birds respond to the urban environment undoubtedly varies by species, this scale was chosen because we expect that this radius is roughly representative of the territory used by most of the observed individuals in this study. Additionally, we examined community composition, functional diversity, and species richness (see below) at multiple radii, from 30 to 1000 m, and this scale of analysis was shown to have the greatest predictive capacity.

To estimate abundance, we adjusted count data for detectability using the R Package unmarked (Fiske and Chandler 2015). We used the generalized distance sampling model of Chandler (2011) to fit yearly and site covariates to adjust abundance estimates by detectability. As birds in

open habitats are more readily observed, we calculated the proportional canopy cover within 50 m of the point count location and used this value as a continuous covariate for detection (Fry et al. 2011). Likewise, because bird activity and habitat associations vary considerably at different stages of the breeding cycle, we included the linear and quadratic terms of Julian day of the point count as a covariate for detectability (McClure and Hill 2012). Because the probability of detection is also dependent on the skill level of the observer, the technician who conducted the count was included as a detection covariate (Sauer et al. 1994). We calculated abundance for each guild and across guilds and used Akaike's Information Criteria, AICc, adjusted by the overdispersion parameter c-hat, to compare models that included only detection covariates and models that contained linear and quadratic terms for impervious surface (Burnham and Anderson 1998).

To test our prediction that species richness will decline with increasing urban land cover, we estimated site-level species richness using Chao's richness estimator (1984) and evaluated richness patterns across the rural-to-urban gradient in a generalized linear model framework in the R. Chao's richness estimator accounts for imperfect detection within what is assumed to be a closed population under the assumption that species with a low number of detections (i.e., singletons and doubletons) are less detectable and will thus be under-represented in raw richness estimates. In its accounting of singletons and doubletons in a sample, and thus between-site variation in detectability, Chao's estimator is expected to provide a robust comparison between sites and has been shown to exhibit low bias and high stability relative to other richness and diversity metrics (see Walther and Martin 2001). Observer, Julian day, and year, as well as an interaction term between Julian day and year, were included as predictor variables for richness. As these variables are considered nuisance terms within this context, the effects of these variables were not directly explored. AICc was used to compare models that included a null of only detection covariates and models that included linear and quadratic impervious surface terms (Burnham and Anderson 1998).

We tested whether there is evidence for environmental filtering within our study region using the community classification tree method of Petchey and Gaston (2002). We constructed a trait matrix using life history traits expected to be predictive of avian response to urbanization (Table 1.1). Categorical traits (i.e., life history guilds) were reclassified as binary variables and weighted by the number of variables required to describe the trait (Laliberte and Legendre 2010). Species by trait distance matrices were calculated in the R package FD (Laliberte et al. 2014) using Gower distances between species, a distance calculation that allows for the combined use of continuous and categorical variables (i.e., guild membership coded as asymmetric binary variables; Podani and Schmera 2006). We constructed a community classification tree for our regional species pool using hierarchical clustering in the *vegan* R package (Unweighted Pair Group Method with Arithmetic Mean; Oksanen et al. 2014; Legendre and Legendre 2008) and calculated the functional diversity (FD) for each community as the sum of branch lengths across species observed at a given site (Petchey and Gaston 2002). Because FD is positively correlated with species richness (Mouchet et al. 2010), we compared observed FD with a null distribution in which tip labels were randomly assigned ($n = 10^4$). This method maintains species richness while randomizing the species assigned to a given tip (Petchey et al. 2007). We then calculated the standardized effect size (SES) for each site as the difference in summed branch lengths between observed and sampled communities divided by the standard deviation of sampled communities. Negative and positive SES values represent communities that are less or more functionally diverse than expected given their species richness. We evaluated the mean and 95 percent confidence intervals of SES values across sites, with values of less than zero providing supportive evidence for the influence of environmental filtering (Mason et al. 2013). To test our prediction that the urbanization filters species as a function of their life history traits, we evaluated SES values across the impervious surface gradient, with the expectation that values will decline with increasing urbanization (Flynn et al. 2010). We used AICc to compare

generalized linear models of SES as a function of linear and quadratic terms of impervious surface and a null model of no effect.

We explored the influence of urbanization on avian guild associations to determine which traits best explain avian community composition across the rural-to-urban gradient. We calculated the relative abundances of guilds for a given life history trait (e.g., nesting guilds) at communities across the rural-to-urban gradient and used binomial regression (logit-link) to model variation in the relative abundances of each guild in response to urban land cover. AICc was used to compare models of linear and quadratic responses to impervious surface to a model of no effect of urban land cover. Because inference is limited by joint membership between guilds and among guilds and niche breadth axes, we explored the correlation structure across both sets of variables.

Results

A total of 44 native bird species and 1,474 individual birds were observed across all sites and years (see Supplemental Table S1.1). Site-level Chao species richness estimates ranged from 5 to 61 species and averaged 18.8 species per site (±0.051). The data support the hypothesis that species richness decreases with increasing urban land cover. Richness estimates peaked at sites with low impervious surface and were their lowest at the most urban sites (Figure 1.1B, Table 1.2). There was considerable model support for a monotonic decline in functional diversity with increasing impervious surface cover (Table 1.2, Figure 1.1C). This pattern supports our prediction that the influence of environmental filtering on avian community composition increases with increased urbanization even after accounting for species richness.

Across guilds, total abundance exhibited a monotonic decline with increasing urban land cover (β = -0.0074, ΔAICc relative to the null = 34.7) and there was no evidence for an increase in abundance across the rural-to-urban gradient for any of the guilds we observed (Table 1.3, Figure

1.2). Insectivorous, foliage and aerial foragers, cavity nesting species, and residents each exhibited steep declines in estimated abundance with increasing urban land cover. Despite our expectations that omnivores and ground foraging species are positively associated with urbanization, the estimated abundances of these species declined with increasing impervious surface. Likewise, while we expected granivores to be positively affiliated with urban environments, the null model that excluded impervious surface received equivalent model support to the model which showed an increase in the estimated abundance with increasing impervious surface for this guild. The estimated abundances of shrub and tree-nesting species, as well as short-distance and Neotropical migrants, exhibited moderate declines across the rural-to-urban gradient but there was no evidence for variation in the estimated abundance of bark foraging species with increasing impervious surface.

There were marked differences in the proportional composition of life history guilds across the rural-to-urban gradient (Table 1.4, Figure 1.3). Omnivores, which made up the largest proportion of diet guilds throughout our study region, increased in relative abundance with increasing impervious cover at the rural end of the urbanization gradient but exhibited levelled off as urban intensity increased. While granivores made up less than 10 percent of the avian community at rural sites, the relative abundance of this guild increased sharply with increasing urban land cover and the relative proportion of this guild was similar to that of omnivores at the most urban sites. Conversely, despite making up nearly 30 percent of the avian community at rural sites, insectivores declined to less than 5 percent of the community at the urban end of the impervious surface gradient. Among nesting guilds, shrub and tree nesting species increased in relative abundance while the relative abundance of cavity-nesting species exhibited a steep decline with increasing urban land cover, despite each guild making up an equivalent portion of the bird community at rural sites. Among foraging guilds, only ground foraging species increased in relative abundance with increasing impervious surface, with substantial model support of a monotonic decline in each of the remaining

foraging guilds. Resident and short-distance migrant species made up equivalent portions of bird communities as the rural end of the urbanization gradient, but exhibited an inverse relationship with impervious surface. Contrary to our expectations, resident species declined in relative abundance with increasing urbanization while short-distance migrants increased. Likewise, while we predicted that Neotropical migrants would be negatively influence by urbanization, there was no evidence of a relationship between the relative abundance and impervious surface, as the null model received the greatest model support for these species.

Discussion

We assessed the influence of urbanization on avian community composition across the rural-to-urban gradient in Greater Washington D.C. Consistent with previous research, we found a decline in species richness and a predictable shift in the structure of avian communities with increasing urbanization. This study is unique, however, in its application of functional diversity to assess whether there is evidence of environmental filtering across the rural-to-urban gradient. As functional diversity was found to decline with increasing impervious surface even after accounting for a decrease in species richness, our results provide strong supportive evidence that urban habitats filter avian communities as a function of their traits (Petchey et al. 2007). As such, this study is the first to show evidence for environmental filtering of species traits along a local-scale gradient of urbanization. While the seminal work of Croci et al. (2008) found evidence for regional variation in avian traits in response to urban environments, they were not able to observe a local-scale filtering effect. A key difference between our studies, however, is that Croci et al. sampled patches of forest within the urban and suburban matrix whereas we sampled from forested patches and from within the matrix itself. We suggest that this may highlight that bird communities may be structured by land cover distributions at the territory scale rather than the influence of surrounding urban land cover.

Species Richness

We observed a decline in species richness with increasing urban land cover, a relationship that has been observed across numerous biogeographic regions (reviewed in Marzluff 2005). Several studies have documented a peak in species richness at intermediate portions of the rural-to-urban gradient (e.g., Blair 2001, Blair and Johnston 2008). This pattern is expected to be indicative of increased richness along ecotones, as avian assemblages are comprised of both urban sensitive and insensitive species at this portion of the gradient (Crooks et al. 2004). While the model of a quadratic relationship between richness and relative abundance was best supported by the data, we found no evidence that species richness was enhanced in suburban environments (Figure 1.1). This may in part be influenced by the removal of non-native species from our analysis. Urban environments have been found to support high densities of non-native species that are able to exploit urban and suburban habitats, such as the House Sparrow (*Passer domesticus*), due to life history characteristics (e.g., omnivorous dietary niche) that are expected to allow them to colonize this portion of the gradient (Lancaster and Rees 1979; Sol et al. 2012). Despite our removal of non-native species, however, there was no observable decline in species richness within exurban (5 - 20 percent impervious surface) or suburban portions of the urban gradient (30 to 50 percent impervious surface, Marzluff 2001) and our findings do support considerable variation in guild structure at these levels of impervious surface. Likewise, addition of non-native species to our data (results not shown) did not change the overall observed trend in species richness, though it did slightly moderate the rate of decline in species richness with increasing urban land cover. Taken cumulatively, however, our results support expectations that observed declines in species richness across the rural-to-urban gradient may be buffered by the replacement of urban-sensitive guilds with those that are less sensitive to urbanization (Crooks et al. 2004; Jokimaki and Suhonen 1993).

Dietary guilds

Our results provide considerable evidence for species sorting based on avian dietary guilds in Greater Washington, D.C. suggesting that food resources may be an important determinant of the persistence of species in urban environments. We observed a decline in the relative abundance of insectivorous birds and an increase in the relative abundances of omnivorous and granivorous dietary guilds across the rural-to-urban gradient. In their review of the effects of urbanization on avian communities, Chace and Walsh (2006), found that urban environments select for omnivorous and granivorous dietary guilds. As the estimated abundance of each of the dietary guilds was negatively associated with impervious surface, however, the observed variation in relative abundances was largely driven by a steep decline in the estimated abundance of insectivorous birds. Indeed, a negative response of insectivores to urbanization has been a geographically widespread phenomenon. For example, Lim and Sodhi (2004) found a decline in insectivores in metropolitan Singapore and Sengupta et al. (2014) observed a similar loss of insectivores in urban environments in India despite high proportions of this guild within exurban landscape (but see Raupp et al. 2010). The substantial decline in the estimated abundance of insectivores suggests that, while urban environments may support higher relative abundances of omnivore and granivores, the dominance of these dietary guilds in previous studies is likely a result of the loss of insectivorous birds at urbanized sites rather than a benefit conferred to these guilds by urban land cover.

Foraging Guilds

Across foraging strategies, only the relative abundance of ground foraging birds, such as the American Robin (*Turdus migratorius*) and Mourning Dove (*Zenaida macroura*), increased with urban land cover and the relative abundances of foliage and aerial feeding species exhibited a steep decline with increasing impervious surface. The observed increase in the relative abundance of ground

foragers has been supported across a number of studies (e.g., Emlen 1974; Lancaster and Rees 1979; Johnston 2001), though we found no evidence that the abundance of ground foraging species varied across the rural-to-urban gradient. Likewise, while there was some evidence for a negative association between the relative abundance of bark foraging species and urbanization, there was no evidence for variation in the absolute abundance of this guild with impervious surface.

Nesting Guilds

We observed a decline in the relative abundance of ground and cavity nesting birds and increase in the relative abundance of tree and shrub nesting guilds with increasing urban land cover. Additionally, there was considerable support for a decline in the absolute abundances of cavity nesting and ground nesting birds, though no evidence for a relationship between tree or shrub nesting birds and impervious surface. This suggests that shrub and tree nesting species may be insensitive to habitat composition in urban environments while cavity and ground nesting species may be filtered by urban land cover. Indeed, Blewett and Marzluff (2005) found that snags and standing dead trees in which cavity nesting species typically build nests, were absent from the human-built environment, leading to an overall reduction in the abundance of this guild in suburban landscapes of Washington state, U.S. The negative association between ground-nesting species has been shown across study regions (reviewed in Marzluff 2001) and is expected to be a result of sensitivity to enhanced rates of predation for this nesting guild (Jokimaki et al. 2000). The observed decline of cavity-nesting species with increasing urbanization, however, is likely context dependent, as many studies have observed no response or even increased abundances of these species in urban environments (e.g., Jokimaki et al. 2000, 2014; Croci et al. 2008).

Migratory Status

The relative abundance of resident species of birds declined markedly with increasing urban land cover while that of short-distance migrants increased and Neotropical migrants showed no response to urbanization. The response of migratory guilds to impervious surface was contrary to our prediction that migrant bird species would decline with increasing urban land cover. Numerous studies have reported a negative association between the presence of Neotropical migrant birds and urbanization (e.g., Stratford and Robinson 2005) and several studies (e.g., McKinney and Lockwood 1999; Kark et al. 2007; Rodewald and Bakermans 2011) have suggested that resident life histories are one of the key features that defines urban-adapted species (but see Evans et al. 2011). For example, Rodewald and Bakermans (2006) found that resident species increased in abundance with increasing urban land cover surrounding riparian forests while the abundance of Neotropical migrant birds were negatively associated. Our ability to detect the influence of urban land cover may have been masked by high abundances of Gray Catbird (Dumetella carolinensis), an omnivorous species that made up more than 50 percent of the abundance of Neotropical migrants and show no observable response to urban land cover. Likewise, while short-distance migrants were shown to increase in relative abundance with increasing urbanization, almost all of the individuals that comprise this migratory guild were American Robin, American Crow (*Corvus brachyrhynchos*), Fish Crow (*Corvus ossifragus*), and Common Grackle (*Quiscalus quiscula*) species that also showed no response to, or even an affinity for, urban land cover.

Across guilds, a clear limitation to our analysis was the extent of co-membership represented by life history guilds across traits (Figure 1.4). Our ability to detect the response of migratory species to urban land cover may have been hindered by co-membership across guilds. Indeed, while residents were shown to respond strongly to the urbanization gradient in regards to both absolute

and relative abundance, nearly half of the observed resident species were insectivorous and more than half were cavity nesters – both of these guild were shown to decline across the rural-to-urban gradient. Likewise, all five of the aerial foragers and seven of the eleven foliage foragers are insectivorous. While this does not negate the potential impact of foraging strategy on avian community structure, it is impossible to distinguish the response of the foraging strategy for these guilds separately from the apparent influence of dietary niche as evaluated. While methodologies exist to determine the influence of individual traits on community structure, the paucity of individuals observed at a given site, undoubtedly due to low detection probabilities for a given sample, limited our ability to employ these methods (see Legendre et al. 1997, Shipley et al. 2006, Brown et al. 2014, Warton et al. 2015).

Conclusion

Several key results in our study suggest that urban environments filter avian communities as a function of their traits. We observed a decline in species richness and decline in functional diversity across the gradient. Likewise, emergent patterns in avian community structure suggest that some life history traits, especially insectivory, were found to be strongly associated with the sensitivity of species to urbanization processes. As such, our results show that development intensity, as measured by impervious surface, is strongly related to avian guild structure and thus observed declines in species richness across the rural-to-urban gradient likely results from environmental filtering by life history traits.

The use of the proportion of impervious surface cover to approximate the urbanization gradient in our study has both strengths and weaknesses. Urbanization is both a spatial and temporal process (Fernández-Juricic 2003) and thus observed patterns of abundance and species richness may mask delayed local extinctions in modified landscapes (extinction debt, reviewed in Kuussaari et al.

2009). While impervious surface provides a gradient of development intensity (Marzluff 2001), urbanization occurs at multiple spatiotemporal scales through which human socioeconomic and environmental systems are linked (Grimm et al. 2008). Landscape context, for example, has been found to considerably influence avian community assembly — thus analysis of bird communities at one scale may miss key features driving avian response at others (Melles et al. 2003). Moreover, the quality of available bird habitat may vary considerably along the urbanization gradient. For example, Degraaf and Wentworth (1986) found that suburban habitats with mature shrubs and native trees supported higher densities of insectivorous birds, with the type of shrubs and trees present, rather than the proportional cover or even size of tree, the best determinant of insectivorous species abundance. Similarly, White et al. (2005) found significantly higher abundances of insectivores in streetscapes composed of native tree species than exotic streetscapes. As our study shows strong associations but considerable variation in avian community assembly across the impervious surface gradient, further analysis of how landscape context, features of local habitat structure and composition, and qualities of the human system explain the variation of birds in response to urbanization may offer key insights into how to manage habitats to mitigate the loss of biodiversity in an urbanizing world.

TABLES

Table 1.1. Life history traits evaluated in this study, the number of species observed for life history guilds, and the expected response to urbanization.

	Trait	Number of species	Urban influence
Nesting guild:	Tree (cup)	18	*Unknown*
	Shrub	9	*Unknown*
	Ground	3	-
	Cavity	14	-
Migratory guild:	Neotropical	16	-
	Short-distance	17	-
	Resident	11	+
Foraging guild:	Aerial	5	*Unknown*
	Foliage	11	-
	Bark	6	-
	Ground	22	+
Dietary guild:	Insectivore	22	-
	Granivore	3	+
	Omnivore	18	+

Table 1.2. Model selection table for models of species richness and functional diversity by impervious surface with estimates for beta coefficients and proportion of explained deviance.

Model		ΔAIC_c	*w*	β_{IMP} (95 % CI)	β_{IMP2} (95 % CI)	Pseudo-R^2
Species richness	IMP+IMP^2	0.00	1.00	4.6 E-3 (-1.6 E-3, 0.011)	-2.7 E-4 (-3.8E-4, -1.6E-4)	0.31
	IMP	24.5	0.00	-0.01 (-0.013, -7.8 E-3)	-	0.28
	Null	241	0.00	-	-	0.05
Functional diversity	IMP	0.00	0.71	-0.029 (-0.038, -0.019)	-	0.15
	IMP+IMP^2	1.77	0.29	-0.022 (-0.047, 3.1E-3)	-1.1E-4 (-5.1E-4, 2.8E-4)	0.15
	Null	30.3	0.00	-	-	0.00

Table 1.3. Model selection table for models of abundance of life history guilds by impervious surface with estimates for beta coefficients.

Model, Abundance		ΔAIC_c	*w*	β_{IMP} (95 % CI)	β_{IMP2} (95 % CI)
Diet, Omnivore	IMP+IMP²	0.00	1.00	0.35 (0.20, 0.50)	-0.46 (-0.61, -0.31)
	IMP	35.1	0.00	-0.07 (-0.13, -0.016)	-
	Null	39.3	0.00	-	-
Diet, Granivore	IMP	0.00	0.40	0.10 (-0.03, 0.22)	-
	Null	0.07	0.39	-	-
	IMP+IMP²	1.29	0.21	0.25 (-0.11, 0.61)	-0.15 (-0.48, 0.18)
Diet, Insectivore	IMP+IMP²	0.00	0.59	-0.46 (-0.74, -0.18)	-0.35 (-0.79, 0.081)
	IMP	0.76	0.41	-0.67 (-0.81, -0.54)	-
	Null	112	0.00	-	-
Nest, Cavity	IMP+IMP²	0.00	0.98	-0.22 (-0.52, 0.072)	-0.66 (-1.1, -0.19)
	IMP	7.42	0.02	-0.62 (-0.75, -0.49)	-
	Null	107	0.00	-	-
Nest, Shrub	IMP+IMP²	0.00	1.00	0.35 (0.15, 0.55)	-0.45 (-0.65, -0.25)
	IMP	18.7	0.00	-	-
	NULL	19.4	0.00	-0.06 (-0.14, 0.011)	-
Nest, Tree (cup)	IMP+IMP²	0.00	0.80	0.21 (0.034, 0.41)	-0.25 (-0.44, -0.07)
	Null	3.49	0.14	-	-
	IMP	5.29	0.06	-0.20 (-0.093, 0.053)	-
Nest, Ground	IMP	0.00	0.76	-3.1 (-5.4, -0.79)	-
	IMP+IMP²	2.43	0.23	-3.0 (-7.9, 1.9)	0.52 (-16, 17)
	Null	8.51	0.01	-	-
Foraging, Aerial	IMP	0.00	0.65	-3.6 (-4.9, -2.3)	-
	IMP+IMP²	1.20	0.35	-4.3 (-6.0, -2.6)	2.6 (-0.43, 5.7)
	Null	62.3	0.00	-	-
Foraging, Ground	IMP+IMP²	0.00	1.00	0.25 (0.12, 0.38)	-0.34 (-0.48, -0.21)
	IMP	24.7	0.00	-0.07 (-0.12, -0.018)	-
	Null	1.07 E3	0.00	-	-
Foraging, Foliage	IMP+IMP²	0.00	0.53	-0.42 (-0.80, -0.051)	-0.42 (-0.99, 0.15)
	IMP	0.25	0.47	-0.68 (-0.85, -0.51)	-
	Null	71.0	0.00	-	-
Foraging, Bark	IMP+IMP²	0.00	0.62	0.74 (0.05, 1.4)	-1.11 (-2.2, -0.019)
	Null	1.58	0.28	-	-
	IMP	3.61	0.10	0.042 (-0.26, 0.34)	-
Migration, Neotropical	IMP+IMP²	0.00	0.46	0.14 (-0.13, 0.42)	-0.26 (-0.54, 0.031)
	IMP	1.07	0.27	-0.083 (-0.19, 0.029)	-
	Null	1.10	0.27	-	-
Migration, Short-distance	IMP+IMP²	0.00	1.00	0.27 (0.092, 0.44)	-0.34 (-0.52, -0.17)
	IMP	13.9	0.00	-0.060 (-0.13, 0.0060)	-
	Null	15.1	0.00	-	-
Migration, Resident	IMP+IMP²	0.00	0.81	-0.13(-0.34, 0.075)	-0.28 (-0.053, -0.027)
	IMP	2.91	0.19	-0.35 (-0.44, -0.25)	-
	Null	57.6	0.00	-	-

Table 1.4. Model selection table for models of relative abundance of life history guilds by impervious surface with estimates for beta coefficients and proportion of explained deviance.

Model, Relative abundance		$\Delta QAIC_c$	w	β_{IMP} (95 % CI)	β_{IMP2} (95 % CI)	pseudo-R^2
Diet, Omnivore	IMP+IMP^2	0.00	0.76	0.28 (0.10, 0.45)	-0.21 (-0.41, -0.034)	0.18
	IMP	2.34	0.24	0.11 (0.038, 0.17)	-	0.12
	Null	9.58	0.01	-	-	-
Diet, Granivore	IMP	0.00	0.73	0.36 (0.24, 0.48)	-	0.10
	IMP+IMP^2	2.02	0.27	0.31 (-0.046,0.0.67)	0.053 (-0.31, 0.40)	0.10
	Null	22.4	0.00	-	-	-
Diet, Insectivore	IMP	0.00	0.67	-0.63 (-0.77, -0.50)	-	0.33
	IMP+IMP^2	1.41	0.33	-0.52 (-0.82, -0.21)	-0.19 (-0.72, 0.26)	0.33
	Null	101	0.00	-	-	-
Nest, Cavity	IMP+IMP^2	0.00	0.78	-0.24 (-0.55, 0.078)	-0.53 (-1.1, -0.041)	0.29
	IMP	2.51	0.22	-0.54 (-0.68, -0.41)	-	0.27
	Null	79.8	0.00	-	-	-
Nest, Shrub	IMP+IMP^2	0.00	0.58	0.29 (0.079, 0.50)	-0.20 (-0.44, 0.035)	0.06
	IMP	0.71	0.41	0.12 (0.043, 0.20)	-	0.05
	Null	7.61	0.01	-	-	-
Nest, Tree (cup)	IMP	0.00	0.73	0.13 (0.054, 0.21)	-	0.05
	IMP+IMP^2	2.05	0.26	0.12 (-0.086, 0.33)	0.014 (-0.21, 0.24)	0.05
	Null	8.86	0.01	-	-	-
Nest, Ground	IMP	0.00	0.70	-2.7 (-5.6, -0.94)	-	0.17
	Null	6.85	0.02	-	-	-
Foraging, Aerial	IMP	0.00	0.66	-3.4 (-7.2, -5.1)	-	0.33
	Null	51.6	0.00	-	-	-
Foraging, Ground	IMP	0.00	0.62	0.10 (0.041, 0.17)	-	0.18
	IMP+IMP^2	1.07	0.37	0.18 (0.017, 0.35)	-0.093 (-0.28, 0.090)	0.20
	Null	8.26	0.01	-	-	-
Foraging, Foliage	IMP	0.00	0.66	-0.56 (-0.74, -0.40)	-	0.14
	IMP+IMP^2	1.35	0.34	-0.39 (-0.76, 0.010)	-0.31 (-1.0, 0.26)	0.14
	Null	34.6	0.00	-	-	-
Foraging, Bark	IMP+IMP^2	0.00	0.62	0.25 (-0.41, 1.0)	-0.99 (-2.4, 0.033)	0.05
	IMP	1.21	0.34	-0.33 (-0.61, - 0.084)	-	0.03
	Null	5.77	0.03	-	-	-
Migration, Neotropical	Null	0.00	0.67	-	-	-
	IMP	2.06	0.24	1.8 E-3 (-0.11, 0.11)	-	0.00
	IMP+IMP^2	4.06	0.09	-0.038 (-0.31, 0.24)	0.049 (-0.27, 0.36)	0.00
Migration, Short-distance	IMP	0.00	0.56	0.17 (0.10, 0.24)	-	0.11
	IMP+IMP^2	0.50	0.44	0.28 (0.090, 0.48)	-0.13 (-0.35, 0.076)	0.12
	Null	18.1	0.00	-	-	-
Migration, Resident	IMP	0.00	0.73	-0.27 (-0.37, -0.18)	-	0.15
	IMP+IMP^2	2.00	0.27	-0.25 (-0.47, -0.018)	-0.037 (-0.33, 0.24)	0.15
	Null	30.6	0.00	-	-	-

FIGURES

Figure 1.1. Variation in species richness (A) and standardized effect size of functional diversity (B) across the rural-to-urban gradient in our study region.

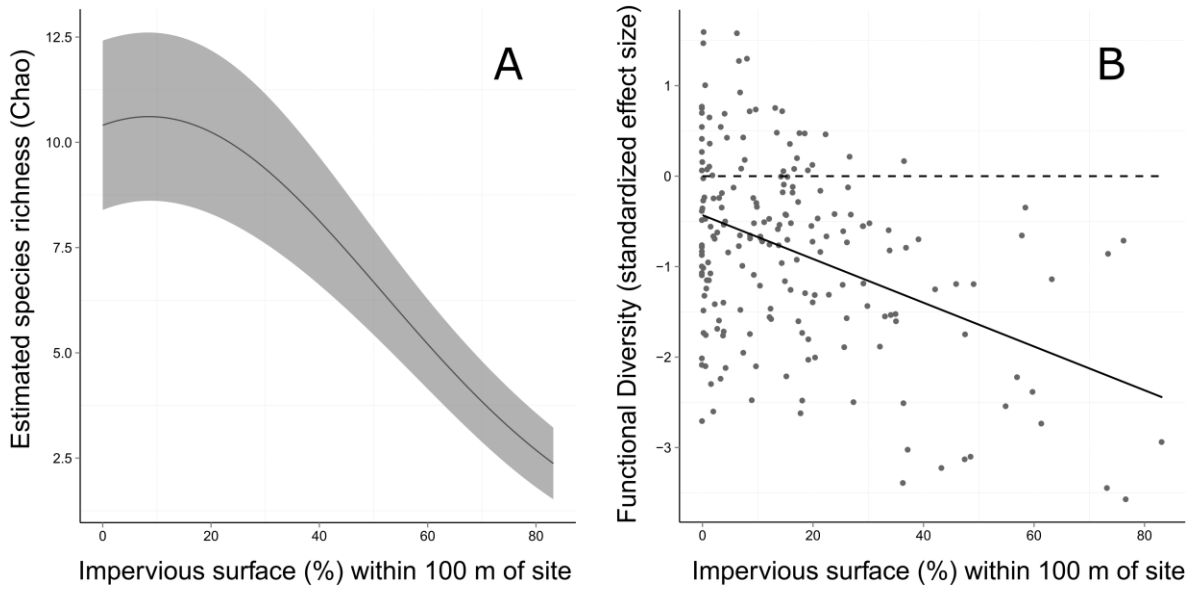


Figure 1.2. Estimated abundance of diet, foraging, nesting, and migratory guilds (rows A through D, respectively) as a function of the proportion of impervious surface within 100 m of each point count. The model estimates for the bark foraging guild are not shown.

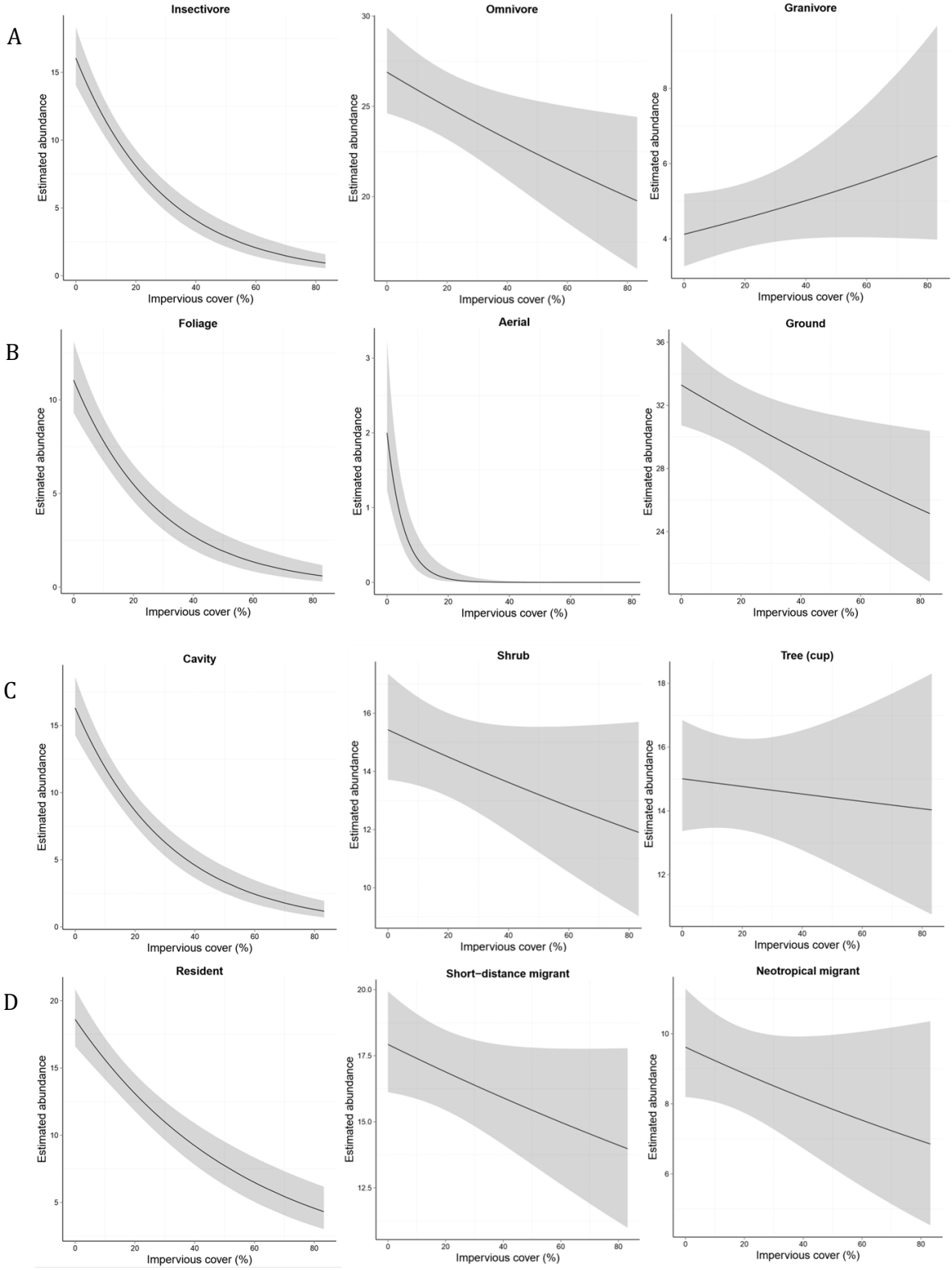


Figure 1.3. Relative abundance of diet, foraging, nesting, and migratory guilds as a function of the proportion of impervious surface within 100 m of each point count.

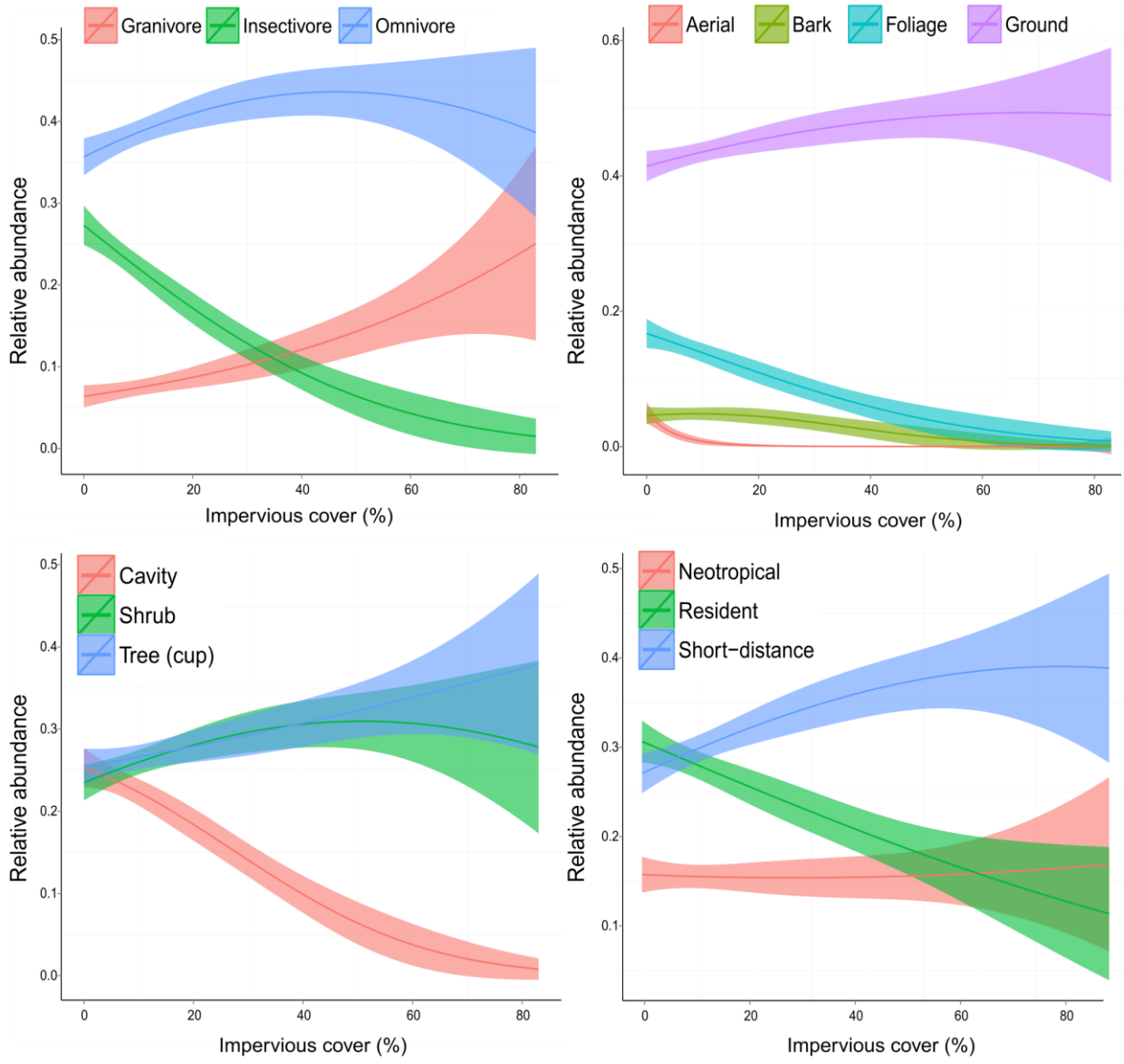
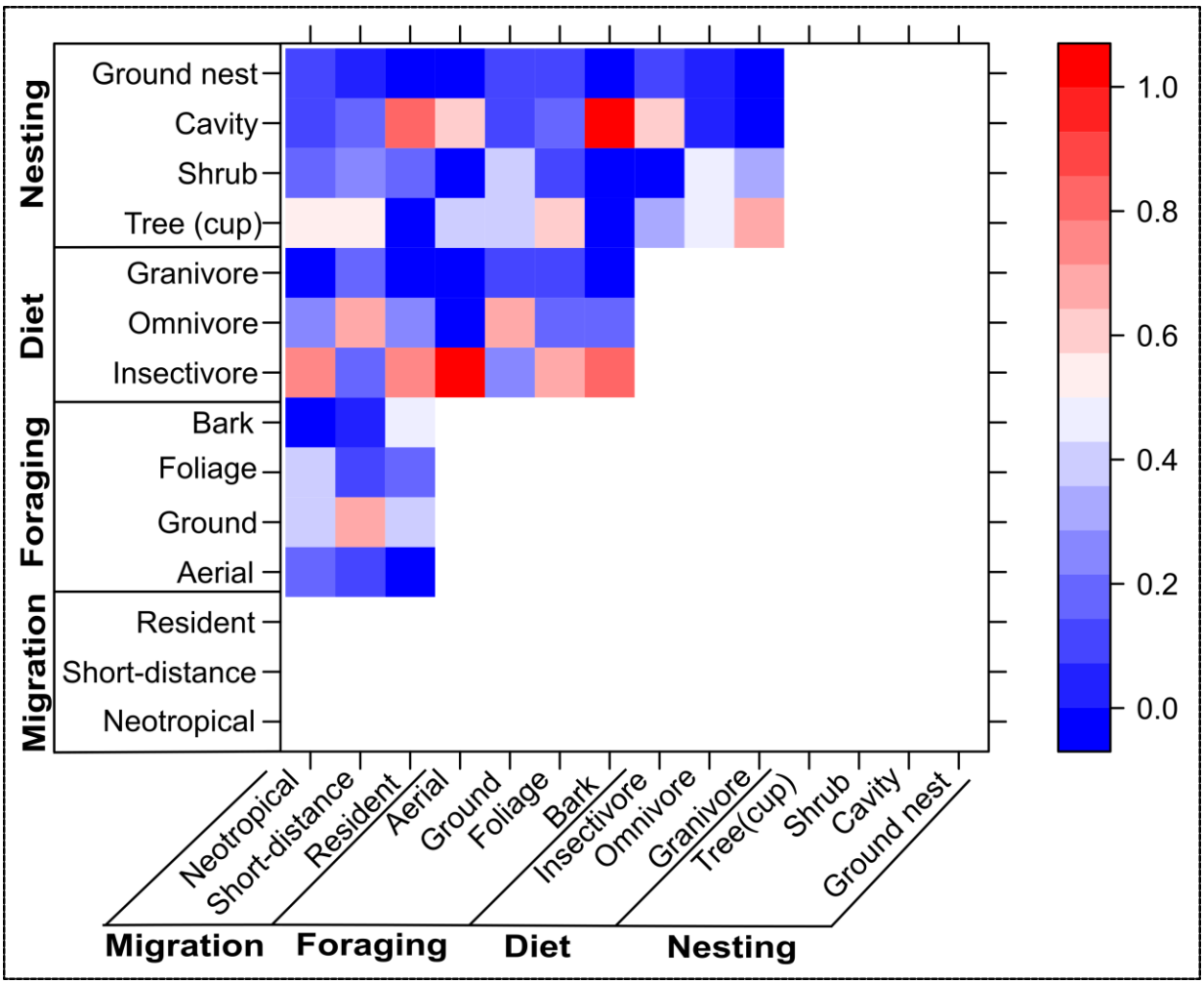


Figure 1.4. Proportion of shared species between life history guilds for birds observed during point counts in the metropolitan Washington D.C. regional species pool. Neither within-trait (e.g., migration) proportions nor diagonal matrix values are shown, as these values are all zero and one, respectively.



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CHAPTER 2: DISPERSAL IN THE URBAN MATRIX: ASSESSING THE INFLUENCE OF LANDSCAPE PERMIABILITY ON THE SETTLEMENT PATTERNS OF BREEDING SONGBIRDS

Introduction

Habitat fragmentation is considered to be one of the primary mechanisms through which the expansion of urban environments has led to a global decline in biodiversity since the middle of the twentieth century (McKinney 2002). As habitats are modified, the area associated with available high quality habitat is often reduced for many species as is the permeability of the landscape thus impeding movement and dispersal of individuals– a process that functionally isolates individuals and populations from portions of the landscape (Andren 1994, Moilanen and Nieminen 2002). The movement of individuals between birthplace and first breeding location (natal dispersal) or between successive breeding locations (breeding dispersal), is seen as critical for the persistence of metapopulations by linking local populations and permitting gene flow across a landscape (Levins 1969, Beier and Noss 1998, Hanski 1999, Clobert 2001, Moilanen and Nieminen 2002). As human-built habitats likely influence patterns of dispersal in many urbanized regions, determining how organisms disperse through such environments provides an important tool for understanding the influence of human-dominated landscapes on wildlife populations (Crooks and Sanjayan 2006).

Dispersal has been traditionally described as a three-step process involving emigration from breeding or natal sites, movement between sites, and settlement to new breeding locations in a subsequent year (Weisser 2001, Bowler and Benton 2005). This process becomes decidedly more complex for migratory species, where conditions on wintering grounds have been found to influence

the condition of individuals and thus the establishment of breeding territories in subsequent years (i.e., carry-over effects, e.g., Studds et al. 2012, Rushing et al. 2015). Even among resident species, costs associated with one stage of dispersal influence subsequent stages as the condition of an individual prior to emigration, the path taken to new breeding locations, and the success of an individual following settlement are interdependent (Stamps et al. 2005, Clobert et al. 2009). For successful dispersal, the benefits of establishing new territories must outweigh the costs associated with increased predation risk, stress, and energy depletion for dispersing individuals (Greenwood and Harvey 1982). While both emigration and settlement are thought to be a function of conspecific density, patch size, predation pressure, and habitat quality, movement is dependent on an organism's perception of the landscape and the ability of an individual to move through the inter-patch matrix (landscape permeability, Baguette and Van Dyck 2007). As such, both the physical arrangement of habitat patches across the landscape and the quality of the inter-patch matrix are expected to be key determinants of whether individuals can successfully disperse between patches (Opdam et al. 1985, Urban and Keitt 2001, Bélisle 2005).

The influence of habitat fragmentation on the movement of organisms has often been considered largely a function of the physical distance between resource patches and the arrangement of those patches within a given landscape (Haila 2002, Ewers and Didham 2006). The extent to which movement may be facilitated or impeded by the resources and conditions associated with the landscape matrix in which habitat patches are embedded has increasingly been recognized as fundamental to the permeability of landscapes (e.g., Taylor et al. 1993, Kupfer 2006, Lindenmayer and Fischer 2006). Moreover, the ability of organisms to move across fragmented urban landscapes, and thus access patches of resources, is contingent both on the quality of the landscape matrix and species-specific response to landscape features (Wiens 1976, Kotliar and Wiens 1990, Pearson et al. 1996). For example, in the study of a single landscape, Bunn et al. (2000) found that the landscape

had high permeability for the American Mink (*Mustela vison*) and low permeability for the Prothonotary Warbler (*Protonotaria citrea*) due to their differential dispersal abilities. Even within a species, movement behavior in response to landscape configuration has been found to vary by age, sex, and position of individuals within a given habitat patch (reviewed in Debinski and Holt 2000).

An organism's response to the landscape during dispersal is also expected to be dependent on its life history traits as well as landscape specific costs and benefits associated with movement, settlement, and the deferred costs following dispersal events (Stamps et al. 2005, Bonte et al. 2012, Burgess et al. 2012). Dispersal events that incorporate exploratory behaviors are expected to minimize dispersal costs as exploration increases the efficiency by which individuals settle in suitable habitat, thus reducing the risk of unsuccessful dispersal – though the increased time spent during dispersal may increase the probability of mortality during dispersal events (Conradt et al. 2003, Baguette et al. 2012). During such dispersal events, it is expected that the distance travelled, the path taken between patches, and settlement decisions will be strongly affected by the distribution and quality of habitat encountered by dispersing individuals (Van Dyck and Baguette 2005). Because of this, patches of suitable habitat that are spatially isolated or located within a matrix of low habitat quality are expected to have a lower probability of settlement. Conversely, if the distance between patches exceeds the perceptual range for a given species or patches are embedded within a low quality matrix, directed dispersal events are expected to predominate and intervening land cover will have little effect on dispersal distance or route (Wolff et al. 1997, Mennechez et al. 2003). Such directed dispersal events may be more energetically costly for dispersing individuals and increase the risk of unsuccessful dispersal despite reducing the risk of mortality during dispersal (Zollner and Lima 1999, Conradt et al. 2003, Bonte et al. 2012).

Studies of the movement of organisms across the landscape have found that land cover features are critical in either constraining or facilitating the movement of individuals across

fragmented landscapes. For example, previous research has demonstrated behavioral avoidance of forest bird species in crossing open habitats (i.e., gap-crossing decisions) between forested patches using simulated territorial intrusion (Awade and Metzger 2008), predation threat (Belisle and Desrochers 2002), and radio-telemetry (Bayne and Hobson 2001). Patterns of seed dispersal by birds have provided proximate evidence that birds utilize corridors of habitat when moving across fragmented landscapes (e.g., Haddad et al. 2003, Carlo et al. 2013). Over larger spatial extents, translocation experiments have provided some evidence for the influence of matrix habitat and the distribution of patches on avian movement (e.g., Kennedy and Marra 2010). At still larger scales, graph models have provided a link between a bird dispersal behavior and the distribution of habitats across landscapes (Bunn et al. 2000, Urban and Keitt 2001, Minor and Urban 2008), however, the applicability of graph models is dependent on the patchiness of the landscape and may be difficult to apply in landscapes with large contiguous patches (Minor E.S., *personal communication*). Despite evidence that land cover mediates movement, however, there are comparatively few studies that empirically link movement and land cover to dispersal events in urban environments (but see Delgado et al. 2010).

Here, we consider the dispersal of four common songbird species to the rural-to-urban gradient of the Eastern United States across landscapes of varying development intensity. Our study species, which include the American Robin (*Turdus migratorius*), the Gray Catbird (*Dumetella carolinensis*), House Sparrow (*Passer domesticus*), and Northern Cardinal (*Cardinalis cardinalis*), represent distinctly different life history strategies and are thus expected to have a differential response to the landscape despite the co-occurrence of these species in similar habitats (see Table 2.1). We address the movement and dispersal of individuals using two levels of inference – a mark-recapture study to assess the influence of landscape permeability on settlement patterns and a translocation experiment to evaluate the influence of land cover on movement. We test the hypothesis that land cover

influences dispersal and settlement patterns by assessing the distribution of previously marked individuals within a 1.5 km radius of six banding stations in the Washington D.C. metropolitan area. We predicted that sites with higher permeability to the banding station will have a higher likelihood of settlement. Because events outside of the breeding landscape have been found to strongly influence the settlement patterns of migrant species (e.g., Rushing et al. 2015), we expected that permeability will be a stronger determinant of the settlement patterns for residents. To test this prediction for each species and landscape, we constructed models of habitat suitability and structural permeability and compared the models of dispersal in which the probability of settlement is weighted towards sites with a higher degree of permeability with those in which likelihood of settlement is associated with the suitability of the settlement site or distributed randomly. We assessed within-species variation in dispersal by evaluating whether there are observed differences in dispersal distance, landscape permeability, and suitability of settlement sites between age classes and sexes. We further examined the influence of land cover on movement by conducting a translocation experiment across landscapes of differing land use intensity with one of our focal species, the resident Northern Cardinal.

Methods

To assess patterns of dispersal, birds banded in previous years at six banding stations in metropolitan Washington D.C. between the years of 2003 and 2011 were resighted during the breeding seasons of 2011 and 2012. Banding stations were representative of rural (Rock Creek Park, Maryland), suburban (Spring and Opal Daniels Parks (Takoma Park, Maryland), Bethesda Maryland), and urban (Foggy Bottom and the National Mall in Washington, D.C.) landscapes. For each banding station, the surrounding area was binned into four distance classes (the banding location, 150-500 m, 500-1000 m, and <1000-1500 m) aligned with the four cardinal directions (see Figure 2.1). Sampling

locations were selected at random from each directional and distance bin with the number of samples per bin stratified by distance such that an equal proportional area was sampled within each bin. As our study region is predominantly composed of privately-owned land, the sample locations were adjusted to the nearest accessible area and a minimum distance of 100 m was maintained between samples. A minimum of twenty minutes was spent searching for color-banded birds within an area of 50 m from the center of the sample using playback of conspecific song and mobbing calls. Re-sighted birds were identified by color bands and their location was recorded using a handheld GPS. Birds resighted during the same year in which they were banded were not included in this analysis.

To evaluate the influence of habitat permeability on settlement patterns, we estimated habitat suitability using point count data and land cover metrics expected to be representative of habitat preference. Point counts were conducted during the breeding season between 2009 and 2012 by technicians as a part of the Neighborhood Nestwatch program at 222 sites across the rural-to-urban gradient within the Washington D.C. metropolitan area (for full description of point count methodology, see Evans 2015, Chapter 1). All spatial analyses were carried out in R using packages *raster* (Hijmans 2015) and *sp* (Pebesma and Bivand 2005, Bivand et al. 2013). Proportional canopy cover and impervious surface (30 m resolution, Xian et al. 2011) were used as proxy variables of habitat suitability. While we acknowledge that these variables do not represent the totality of habitat variation along the rural-to-urban gradient, these land cover metrics have been shown to be predictive of avian nest success (canopy cover and impervious surface, Ryder et al. 2011), adult survival (impervious surface, Evans et al. 2015), and community composition (impervious surface, Evans et al. 2015, Chapter 1). We calculated the proportional cover of land cover variables within a 3 x 3 cell neighborhood moving window. Because several of our species are considered to be edge specialists, for each 3x3 cell neighborhood we also calculated the standard deviation of canopy cover

values. This metric is considered a continuous analogue of categorical habitat heterogeneity (McGarigal et al. 2009) as high standard deviation in canopy cover values relates to habitats associated with forest edges (see McGarigal et al. 2009).

We used logistic regression to model the habitat suitability for each species as a function of the presence-absence of the species at a given site in response to our land cover metrics. While we acknowledge the importance of incorporating detectability for modelling occupancy, due to sample size constraints and the high prevalence and detectability of our focal species, we were not able to include detectability within our suitability models. Due to uneven sampling across sites, site-level observations were weighted by the number of samples per site. As species may show a differential response to canopy cover at different levels of development and degrees of heterogeneity, interaction terms were included between these variables and proportional canopy cover. Because species may not have a linear effect to land cover variables, for example if species experience peak occupancy at intermediate levels of proportional canopy cover, we included quadratic terms for each variable. Habitat suitability was estimated and projected as a raster for the individual focal species and landscapes surrounding banding stations, with values ranging from zero, for unsuitable habitat, to one for suitable habitat. (see Figure 2.2).

Habitat suitability models were used to estimate the permeability from the banding station to sampling locations using the package *gDistance* (van Etten 2015). We calculated a transition matrix between adjacent raster cells (queen's case) weighted by the inverse of the habitat suitability rasters — thus suitability provides a measure of conductance between cells (see McRae et al. 2008). Transition matrices were used to develop a cost distance raster representing the random-walk distance, in meters, between the banding station and all surrounding cells. Cost distance and habitat suitability raster values were then extracted to each sampling location. Because cost distance

increased and the prevalence of resighted birds decreased as a function of the Euclidean distance from the banding station, we defined the expected habitat permeability for a given location as the ratio of the cost distance and Euclidean distance between the banding station and each sample (See Figure 2.2).

To test our prediction that habitat permeability influences settlement patterns, we compared models of dispersal in which samples were occupied by banded birds as a function of the habitat suitability of the settlement location and the permeability between the banding station and sampling location for each banding station. Sampling locations around each banding station were subset such that samples within 150 m of the center of the banding station were not considered to have dispersed. This distance, while conservative, may be representative of within-territory movement of birds maintaining the same territories in subsequent years – thus patterns of observations of previously banded birds in this distance range likely result from biological processes other than dispersal. Additionally, one site (Spring Park, Takoma Park, M.D.), included a net location 180 m from the banding centroid – as there was no record of which birds were banded at this location, samples within 150 m of either location were removed from the analysis. Additionally, as maximum dispersal distances varied by site and species, and banded birds were not observed across all distance classes, we subset samples to only those within the maximum observed distance for a given site and species to avoid biasing our results by including unoccupied samples outside of the observed dispersal distances. Standardized effect sizes for permeability and suitability were calculated for each banding station as the difference between observed sample values and a random sample of values (n = 100) for each banding stations sampling region divided by the standard deviation of sample values (see Figure 2.4). Because there was variation between banding stations in suitability and permeability, we calculated z-scores for our suitability and permeability metrics for each banding station separately, thus the land cover values for each sample is provided relative to the other samples

within the banding stations sampling region. We assessed a candidate set of logistic regression models that included habitat suitability, permeability, additive and interaction terms with both predictors, as well as a null model with only the intercept term. Akaike's Information Criteria, adjusted for small sample size, were used to determine the model best supported by the data. The relative weight of evidence for between two given model was calculated as ratio of Akaike weights between models (Burnham and Anderson 1998).We used Mann-Whitney tests to explore the variation in permeability, suitability, and the distance of individuals from the banding station of each sex and age class.

We further explored the influence of land cover on dispersal by conducting a translocation experiment across three landscapes representing rural, suburban, and urban land uses. We conducted the experiment on eight male Northern Cardinals during the breeding seasons of 2011 and 2012. Northern Cardinals were chosen because they were the most frequently re-encountered birds among our focal species. On each bird, we attached a 0.39 g VHF radio transmitter (Advanced Telemetry Systems, Isanti, MN) using a backpack harness of elastic thread. Birds were translocated 1.5 km from the capture location across one of eight pre-determined landscapes, and tracked twice per day following release. The location of the bird was determined using triangulation and, when possible, visible identification of the individual. To assess the influence of intervening land cover on movement, we then evaluated the days-to-return for each individual. Due to sample size constraints, however, we were not able to conduct a formal statistical analysis of the results of this experiment.

Results

Among 3,606 identifiable individuals that were banded at the six stations between 2003 and 2011, a total of 210 birds were re-encountered in this project, with 188 individuals able to be

identified to banding location (Table 2.2). Nearly half of the observations were at a distance of less than 150 m (n = 85) and were therefore not included within further analyses.

Habitat suitability models (Figure 2.2) developed from point count data yielded varying results, with marked differences in the proportion of explained variance and average predicted suitability values across our focal species. Models of House Sparrow and Northern Cardinal had considerable explanatory power, explaining 26.9 and 37.7 percent of the variance in observed occupancy, respectively. Our study region had considerably higher predicted suitability for the Northern Cardinal, with an average suitability across the study region of 0.54 (Supplemental Figure 1), than the House Sparrow, with an average suitability of 0.34. The model for the American Robin explained 16.2 percent of the variation in observed occupancy with an average suitability of 0.53 across the study region. The model of the Gray Catbird yielded the lowest explanatory power, explaining only 11.9 percent of the variance. Moreover, the study region had an overall mean suitability of 0.76 for the catbird, suggesting that our study region was, overall, very suitable for this species relative to the other focal species given the explanatory variables used in this analysis (Figure 2.3).

Species showed a differential response to landscape permeability and habitat suitability, with supportive evidence for our prediction that patterns of settlement would reflect the permeability between banding and resight locations for two of our four focal species (Table 2.3, Figure 2.4). There was considerable model support that Northern Cardinal settlement was higher in sites with high habitat permeability ($\beta = 1.07$, CI: 0.34 to 2.17, pseudo-$R^2 = 0.15$). The model that included the permeability variable alone received 1.72 times the support of the next best model, which included an additive term with habitat suitability, and 6.48 times the support of the best model that excluded the permeability term. There was some model support that permeability positively influenced the

likelihood that sites would be settled for Gray Catbird ($\beta = 0.63$, CI: 0.02 to 1.38). Though the permeability model received 2.4 times more support than the model including both permeability and suitability, and 2.8 times more support than the null model, the model explained little of the variation in the data (pseudo-$R^2 = 0.06$). The data did not provide evidence that permeability influences the settlement patterns of American Robin and House Sparrow, as the null and permeability models received equivalent support for both species. There was no evidence for differences between sex and age classes in regards to distance of individuals from the banding station, habitat suitability of settlement site, nor habitat permeability between settlement and banding station (Table 2.4). Analysis of an age effect for the American Robin was not possible, as only adult individuals were observed outside of the banding area. Additionally, the banding location for several juvenile catbirds and cardinals could not be identified because these individuals were not color-banded.

Our translocation experiment provided supporting evidence that movement patterns of the Northern Cardinal are influenced by intervening land cover. Cardinals translocated 1.5 km over suburban landscapes returned in one and three days, whereas those that were moved over forested landscapes returned in five and seven days and those moved over urban landscapes returned in nine and fourteen days. We were not able to observe a return for two of the eight individuals, one translocated across a forested habitat matrix and the other across a suburban matrix. We tracked movements over a portion of the route for both of the suburban cardinals and one of the urban cardinals. Suburban movements predominantly followed patches of forest edges, when available, to the capture location. The urban Cardinal moved a distance of roughly 0.5 km on the day following release and remained at that site for eight days until travelling back to the capture location in less than an eight hour period during which we were not able to observe the individual movement.

Discussion

This study addresses the influence of land cover on the dispersal of birds in rural, suburban, and urban landscapes using two levels of inference — we assess patterns of settlement of migrant and resident birds one or more years after banding, and the return time of Northern Cardinal individuals translocated across each matrix type. The settlement patterns of banded Northern Cardinal and Gray Catbird, in relation to the habitat suitability and permeability of the landscape, provide considerable support for our prediction that landscape permeability influences the dispersal of individuals across a human-dominated landscape. In conjunction with the results of our translocation experiment, habitat characteristics of the locations where marked individuals were observed in subsequent years suggests a strong link between the distribution of land cover and the functional permeability of landscapes (Tischendorf and Fahrig 2000, Schooley and Wiens 2003, Kindlmann and Burel 2008).

While the sample size of translocated individuals did not allow for statistical analyses of return time, our results are comparable to previous translocation experiments. For example, Kennedy and Marra (2010) found the return time and success of translocated American Redstart (*Setophaga ruticilla*) and Jamaican Todies (*Todus todus*) was dependent on matrix habitat, with the time-to-return for individuals increasing with the intensity of anthropogenic land use. Similarly, Castellon and Sieving (2006), who translocated Chucao Tapaculo (*Scelorchilus rubecula*), an understory species, through open, shrub-dominated, and wooded corridor habitats, found open habitats constrain the movement for individuals of this species. In our study, Northern Cardinals were observed to have the shortest return time when moved across suburban habitats, which reflect high estimated habitat suitability, with moderate return times across forested habitats and the longest return time across the urban landscape, which reflect moderate and low estimated habitat suitability, respectively. The

influence of forested landscapes on cardinal return time especially underscores the species-specific nature of landscape permeability as Northern Cardinal tend to occupy forest edge and open or shrub-dominated habitats within our study region — it would therefore not be expected that a forested landscape would be highly connected for this species (see Wiens 1989, Pearson et al. 1996).

The permeability of habitats may influence patterns of dispersal if individuals exhibit behavioral avoidance of the landscape matrix (i.e. matrix resistance and boundary effects, Haddad 1999, Ricketts 2001) or if movement occurs as a corollary to routine behavior, such as foraging (Baguette and Van Dyck 2007). While our data support the hypothesis that settlement occurs at a higher proportion in sites connected by habitat, observations of the gap-crossing behavior of the Northern Cardinal, suggest that individuals of this species do not avoid gaps and thus do not exhibit behavioral avoidance of the landscape matrix (Grubb and Doherty 1999). Likewise, translocated Northern Cardinals within the current study were observed to travel greater distances when intervening land cover was of low suitability, even when locations were available (e.g., shrub or tree perches) to minimize the flight distances. To our knowledge, while post-breeding periods have been found to involve considerable landscape exploration (e.g. Rappole and Ballard 1987, Heise and Moore 2003) the behavioral response of these species to habitat configuration is largely unexplored. Moreover, we acknowledge that behaviors, such as conspecific attraction, likely influence settlement decisions (Danielson and Gaines 1987). It therefore remains uncertain which mechanisms influence the observed settlement patterns, especially as the path taken between breeding patches cannot be known within this context. Likewise, low reencounter rates may suggest that our study was necessarily biased towards short-distance dispersers, which are expected to be more responsive to landscape pattern, thus there may be multiple behavioral strategies driving movement within our sampled population (Van Dyck and Baguette 2005).

Though we failed to observe a direct effect of habitat suitability on settlement patterns, the lack of influence of suitability on the observed settlement patterns is representative only of resighted individuals, not of the occupancy distribution as a whole. Indeed, samples both with and without resights spanned a range of suitability values and most of the observed sample locations for a given species were occupied by unbanded individuals of that species. The exception to this was the House Sparrow, for which unbanded individuals were not observed outside of sites with considerable human development. Indeed, due largely to constraints in following individuals throughout the dispersal process, and throughout a bird's annual cycle, there remains considerable uncertainty in regards to how individuals respond to landscape-level processes.

Patterns of settlement for the American Robin and House Sparrow were not shown to be strongly influenced by either measure of permeability or habitat suitability. Lack of observed response may be driven by the high degree of permeability in landscapes in which individuals were observed — for example, the House Sparrow was resighted in the greatest numbers in the landscape surrounding the National Mall banding station, an area with high suitability and permeability values throughout. Conversely, the lack of observed response may be driven by a differential behavioral response to the landscape, as House Sparrow have been shown to exhibit low predator avoidance behavior relative to native species (Tsurig et al. 2008), or a response to the landscape that occurs at a wider spatial grain and extent than observed in this study. Indeed, as the home range size of the resident House Sparrow during the breeding season is estimated to encompass several kilometers (Bennett 1990) and previous findings have shown low rates of dispersal for this species (Altwegg et al. 2000, Pärn et al. 2009), the distribution of resighted individuals may represent movement within an individual's home range rather than a dispersal event. Likewise, while the American Robin typically holds territory sizes roughly equivalent to the Northern Cardinal and Gray Catbird during the breeding season, subsequent to breeding this species often forms wide-ranging foraging flocks

(Vanderhoff 2014, Rodewald 2015), which, if the sampled population includes residents, may increase individual's perceptual range of their environment. Cumulatively, the results for both species emphasize the necessity to address, and further explore, the scale by which an organism uses the environment prior to determining the influence of landscape composition on dispersal (Wiens 1989).

The breeding status of observed birds represents another confounding factor in assessing the patterns of dispersal. The high capture and low resight rates across species and banding stations may suggest that populations of banded birds may include many non-territorial individuals (i.e., "floaters", Brown 1969). As such, while these individuals may have been observed to have exhibited movement between seasons, they cannot be considered to have "dispersed" *per se* unless the movement was from previous natal or breeding territories and a new breeding territory was established (Clobert 2001). If this is the case, observed movement between patches may overestimate the biological relevance (i.e., connected metapopulations) of functional connectivity, especially if the locations of captured or resighted individuals are functionally dissimilar to successful breeding locations (Penteriani et al. 2011). As such, further research is necessary to determine the status of birds both before and after dispersal events.

The functional connectivity of landscapes is increasingly recognized as a critical component for consideration for biological conservation (Wiens 1997). Overall, for two of our four focal species, our results support the hypothesis that the structural connectivity of landscapes is a determinant of patterns of dispersal. While we acknowledge that patterns of settlement are not representative of the path taken between banding station and settlement location and, likewise, translocation experiments may not adequately reflect the behavior of organisms during dispersal, our results offer key evidence of the influence of land cover on the dispersal of birds in urbanized

environments. With recent technological advancements in the study of birds, it is now becoming feasible to track individuals throughout a bird's annual cycle — including the processes of emigration, movement, and settlement that comprise dispersal events (see Bridge et al. 2011, Hallworth and Marra 2015). Such advancements will greatly increase our understanding of the influence of landscape composition on dispersal. To date, few have addressed patterns of dispersal across urban environments (see LaPoint et al. 2015) and research on the influence of fragmentation on birds has reflected a strong bias towards forested environments and forest specialist species (Bayard and Elphick 2010). As ecological patterns in forested habitats may not be applicable across habitat types (see Rudnicky and Hunter 1993), the current study provides an important step towards understanding of the influence of humans on landscape-level processes that help shape bird populations and communities.

TABLES

Table 2.1. Life-history traits of the four focal species used in this study.

Species	Migration	Primary Diet	Habitat	Native status
American Robin	Short-distance migrant	Insect, Fruit	Open woodland	Native
Gray Catbird	Neotropical migrant	Insect, Fruit	Shrub-Open woodland	Native
House Sparrow	Resident	Seeds, Insect	Developed land	Introduced
Northern Cardinal	Resident	Seeds, Fruit	Edge-Open woodland	Native

Source: Rodewald 2015

Table 2.2. Samples of focal species across each of the six banding stations. Resights represent the total banded birds encountered across distance classes. Only birds resighted at a distance of greater than 150 m from the banding station were considered to be dispersed and used in dispersal analyses.

Species	Samples	Spring Park	Opal Daniels	National Mall	Foggy Bottom	Rock Creek	Bethesda	**Total Individuals**
American Robin	Banded	218	142	168	173	58	121	663
	Resights	8	10	9	9	0	2	38
	Resights >150 m	2	6	2	3	0	2	**15**
Gray Catbird	Banded	270	189	95	132	167	267	752
	Resights	20	14	5	7	0	7	53
	Resights >150 m	7	10	0	3	0	5	**25**
House Sparrow	Banded*	279	152	348	312	1	181	1273
	Resights	8	0	24	12	0	0	44
	Resights >150 m	3	0	9	4	0	0	**16**
Northern Cardinal	Banded	379	57	11	24	346	128	945
	Resights	26	11	0	3	9	4	53
	Resights >150 m	15	7	0	2	3	2	**29**

*Note: Banding counts for House Sparrow represent the number of uniquely color-banded individuals rather than total captures.

Table 2.3. Logistic models of the likelihood of settlement as a function of habitat suitability, permeability, and additive and interaction terms between the variables.

Species	Model	K	AICc	ΔAICc	*w*	LogLik
American Robin	Null	2	47.0	0.00	0.33	-22.5
	Permeability	3	47.6	0.52	0.26	-21.8
	Additive	3	48.0	0.98	0.20	-21.0
	Suitability	4	49.0	1.95	0.13	-22.5
	Interaction	5	49.9	2.90	0.08	-21.0
Gray Catbird	**Permeability**	3	70.8	0.00	0.46	-33.4
	Additive	4	72.5	1.73	0.19	-33.3
	Null	2	72.9	2.09	0.16	-35.5
	Interaction	5	73.5	2.66	0.12	-32.7
	Suitability	3	74.8	4.04	0.06	-35.4
House Sparrow	Null	2	62.8	0.00	0.36	-24.1
	Permeability	3	63.7	1.08	0.27	-23.3
	Suitability	4	64.5	2.44	0.22	-23.5
	Additive	3	64.9	3.73	0.10	-23.3
	Interaction	5	66.9	4.56	0.04	-23.3
Northern Cardinal	**Permeability**	5	109	0.00	0.48	-25.3
	Additive	3	110	1.08	0.28	-24.9
	Interaction	4	111	2.44	0.14	-24.6
	Suitability	3	122	3.74	0.07	-27.2
	Null	2	123	6.73	0.02	-29.3

Table 2.4. The distance from the banding station and z-scores for habitat suitability and permeability for resighted juveniles, adults, males, and females across sites. Test statistics, *W* and p-values, represent Mann-Whitney test output for differences between age and sex classes.

Species	Age, Sex	n	Mean Distance from banding station (m)			Habitat suitability (z-score)			Habitat connectivity (z-score)		
			$\bar{x}$	*W*	*p*	$\bar{x}$	*W*	*p*	$\bar{x}$	*W*	*p*
American Robin	Juv.	0	-	-	-	-	-	-	-	-	-
	Adult	9	680 ± 97			0.15 ± 0.27			0.55 ± 0.28		
	F	3	687 ± 168	9.5	1.0	0.002 ± 0.47	7.5	0.80	-0.04 ± 0.65	3.5	0.19
	M	6	676 ± 130			0.23 ± 0.36			0.85 ± 0.23		
Gray Catbird	Juv.	7	796 ± 67	42	1.0	0.13 ± 0.26	41	0.97	0.49 ± 0.31	36	0.64
	Adult	12	693 ± 104			0.11 ± 0.20			0.47 ± 0.13		
	F	7	836 ± 94	26	0.57	0.16 ± 0.22	20	0.89	0.26 ± 0.19	13	0.25
	M	6	566 ± 171			0.12 ± 0.33			0.60 ± 0.16		
House Sparrow	Juv.	6	484 ± 76	21	0.75	0.47 ± 0.20	19	0.56	0.36 ± 0.30	20	0.65
	Adult	8	523 ± 136			-0.19 ± 0.45			0.03 ± 0.38		
	F	7	549 ± 153	20	0.89	-0.07 ± 0.38	16	0.47	0.02 ± 0.36	16	0.25
	M	6	513 ± 56			0.26 ± 0.49			0.34 ± 0.41		
Northern Cardinal	Juv.	6	352 ± 100	70	0.20	0.66 ± 0.21	40	0.44	0.98 ± 0.28	44	0.62
	Adult	17	452 ± 48			0.37 ± 0.17			0.39 ± 0.22		
	F	9	383 ± 0.70	49	0.54	0.70 ± 0.18	84	0.09	0.57 ± 0.25	60	0.95
	M	13	472 ± 69.3			0.23 ± 0.19			0.50 ± 0.28		

FIGURES

Figure 2.1. Sampling points are randomly placed within stratified distance and directional bins with the number of samples per bin increasing with distance from the banding station.

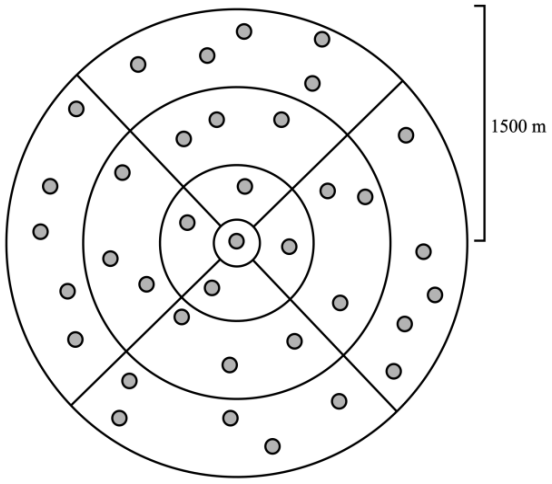


Figure 2.2. Example habitat suitability and permeability raster maps, in addition to sampling locations with and without resighted individuals for each of our four focal species surround the

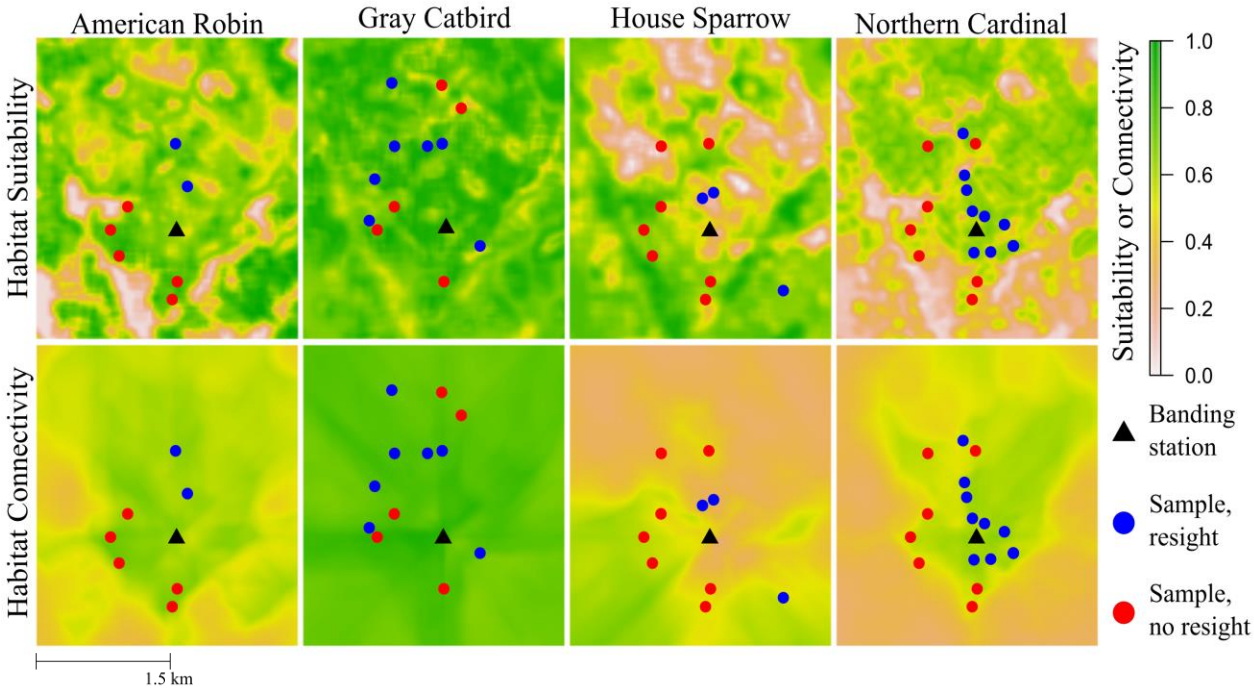


Figure 2.3. Histograms representing the density of predicted habitat suitability for each species across our study region.

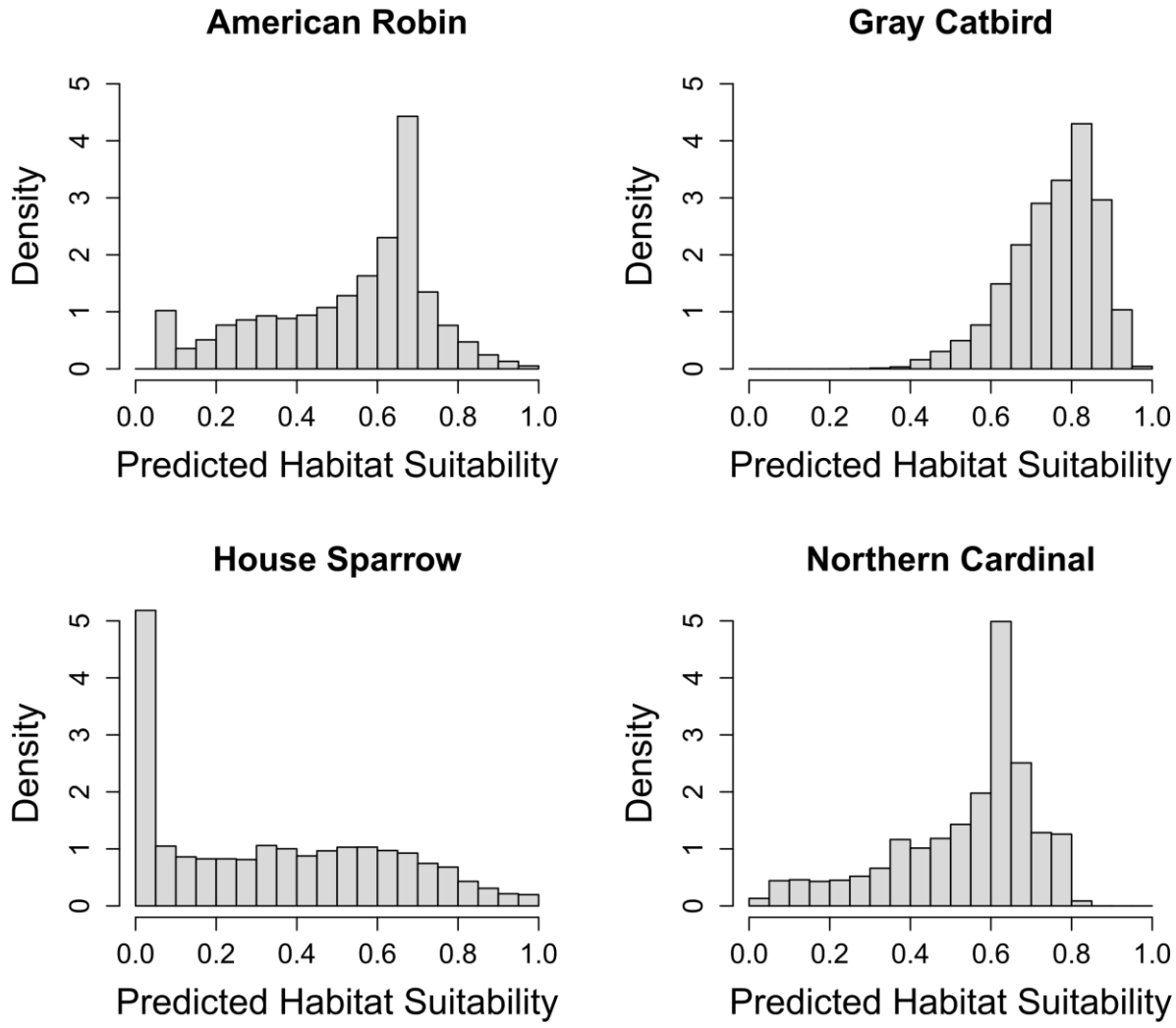
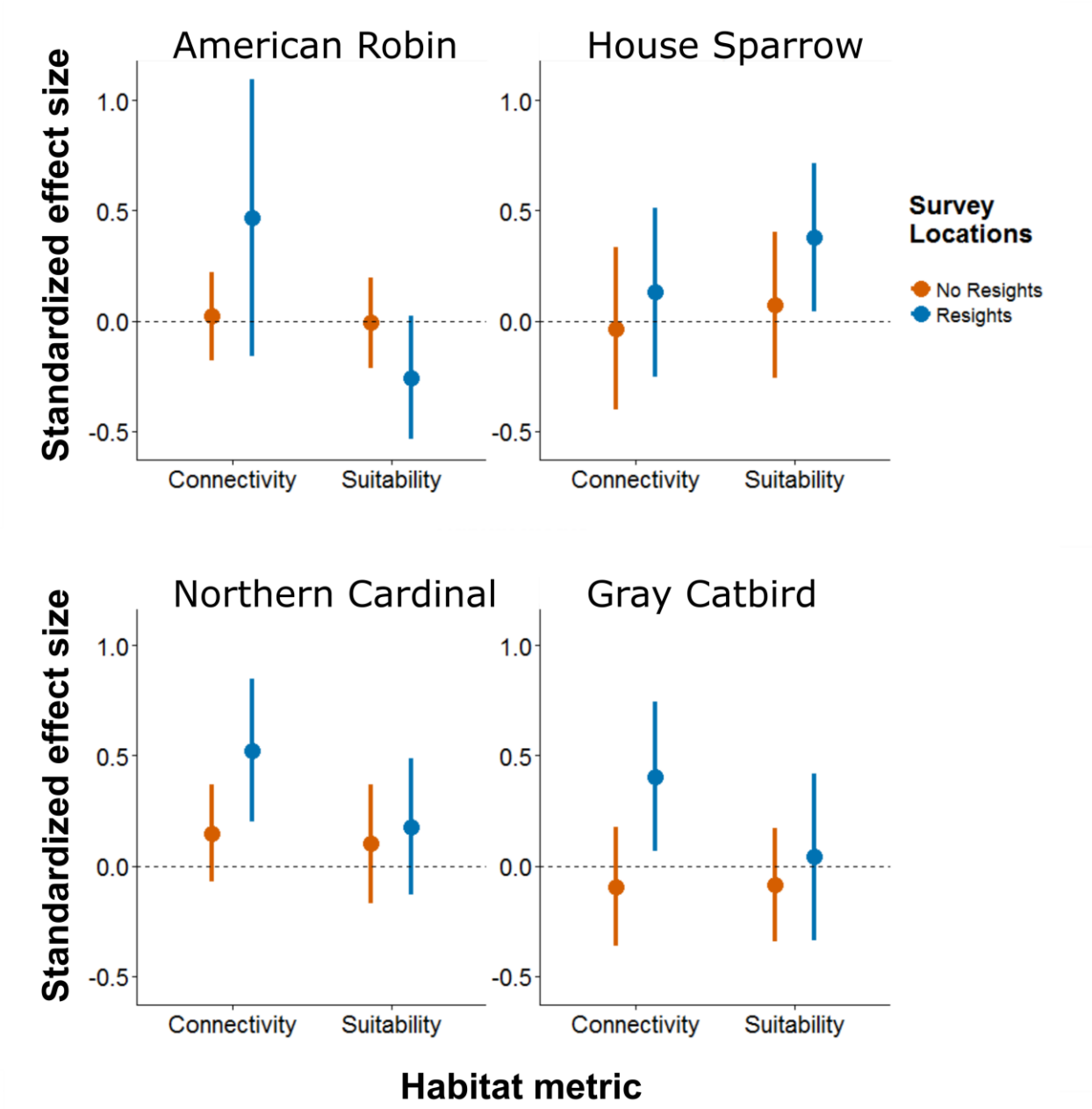


Figure 2.4. Habitat connectivity and suitability of sites in which birds were resighted or in which no banded birds were observed. Standardized effect sizes represent habitat connectivity and suitability values for each banding station, with values above zero representing samples with high suitability or connectivity.



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CHAPTER 3: CHARACTERIZING AVIAN SURVIVAL ALONG A RURAL-TO-URBAN LAND USE GRADIENT

Introduction

Urbanization during the latter half of the twentieth century has altered habitats, restructured avian communities, and influenced the range sizes and population dynamics of animal species (Mckinney and Lockwood 1999, Marzluff 2001, Chace and Walsh 2006). The unique characteristics of human-built environments confers a conflicting set of benefits and challenges that make it difficult to determine whether urban habitats are advantageous or constitute demographic sinks (Gates and Gysel 1978) for bird populations. As the developed land area in the United States is projected to nearly double between 2000 and 2025 (Alig et al. 2004), understanding how organisms respond to these habitats is of paramount importance. Despite the urgency of the problem for conservation, however, the population level consequences of urbanization on birds remain poorly understood (Shochat et al. 2006).

It is hypothesized that anthropogenic habitats may influence bottom-up controls on the distribution and abundance of populations of birds by affecting the resources that determine whether species are able to exist in these habitats (Shochat et al. 2010). Human-dominated environments often contain an abundance of consistent food resources for many species of birds. For example, supplemental feeding by humans, especially for overwintering resident birds, has been found to be positively associated with adult survivorship for a number of granivorous synanthropes (Doherty and Grubb 2002). Moreover, supplemental feeding has been hypothesized to be a primary

driver in the northward range expansion of some seed-eating species, such as the Northern Cardinal (*Cardinalis cardinalis*) because it relaxes winter starvation (Robb et al. 2008). Likewise, human-dominated landscapes are also often dominated by ornamental and invasive species, which have been found to provide essential resources for frugivorous bird species during winter months and thus may facilitate winter survival (e.g., Leston and Rodewald 2006, McCusker et al. 2010). The low temporal variability of resources in anthropogenic habitats is also hypothesized to support higher densities of individuals because they can persist in a state of reduced body condition relative to their rural counterparts (the Credit Card Hypothesis, Shochat 2004). Viewed cumulatively, the abundance and quality of avian food resources is expected to vary spatially along this gradient with resource subsidization as the primary driver of higher food availability at intermediate degrees of urbanization (Raupp et al. 2010).

The benefits of anthropogenic resources, however, may be offset by the fitness costs associated with increased competition and the quality of resources available. For instance, plant communities dominated by non-native species may support lower concentrations of protein-rich arthropod resources (Tallamy 2004), which are necessary for nestling and fledgling development (Atchison and Rodewald 2006, Chamberlain et al. 2009). This may lead to lower nestling survivorship, poorer fledging quality, and structurally smaller adults (Liker et al. 2008). This may lead to lower reproductive fitness of individuals in human-dominated landscapes despite higher rates of adult survival. Therefore, while the temporal and spatial distribution of these anthropogenic resources allow some synanthropes to maintain high densities in urban habitats, it also may result in fitness trade-offs and differential selection for specific life history stages and traits (Shochat 2004).

Similarly, the resource advantages of urbanization for some species may be offset by top-down controls imparted by unique hazards associated with urban environments (e.g., predation, contaminants and disease). For example, birds may experience higher rates of predation in urban

environments due to high densities of small and medium-sized mammalian predators (Crooks and Soule 1999), novel human-subsidized predators (e.g., domestic or feral cats, Balogh et al. 2011, Loss et al. 2013), and locally high densities of raptors and corvids (Chace and Walsh 2006). Collisions with manmade objects, such as buildings and automobiles, are another threat expected to be a significant source of mortality for urban birds (Chace and Walsh 2006). Urban bird populations are also exposed to higher levels of pollutants, such as lead (Roux and Marra 2007), that could negatively affect vital rates. Finally, rates of disease transmission are also higher in urban areas (Kilpatrick 2011), with the effects potentially exacerbated by increased avian densities around common resources such as bird feeders (Robb et al. 2008).

Despite evidence that urban environments can present opposing selection pressures, our understanding of the processes and mechanisms that regulate species persisting in urban landscapes are poorly studied. Research to date on certain life history stages (e.g., post-fledging survival, Whittaker and Marzluff 2007, Ausprey and Rodewald 2011 and nestling survival, Ryder et al. 2010) have failed to document the negative impact of urbanization. Despite its importance for population demography, adult survival is rarely estimated along the rural-to-urban land use gradient, in part because it is data-intensive, requiring multiple years of data collection. To date, most studies on the impacts of urbanization on adult survivorship have compared rural and urban populations (e.g., Horak and Lebreton 1998) or examined forested patches embedded within the broader matrix (e.g., Rodewald and Shustack 2008). These studies have found little or no effect of urbanization on adult survivorship. No studies have yet to be conducted across the continuous rural-to-urban land use gradient from within the urban and suburban matrix habitat. Ultimately, studying the survivorship of urban birds from directly within the urban-suburban matrix is necessary for understanding the demographic consequences of urbanization because these species achieve peak densities in this habitat context (Ryder et al. 2010).

Here we test two mutually exclusive hypotheses about the processes that regulate annual adult survivorship of seven urban-adapted bird species using mark-recapture and resight data. Given that top-down processes are complex in urban environments, variation in ecological pressures across the urbanization gradient can produce differential patterns of avian survival. If top-down processes such as disease, collision or pollution are the primary drivers of variation in survival, we predict reduced survival in urban environments. Likewise, if alternative top-down process such as predation by domestic cats (Balogh et al. 2011) drives patterns of survival we predict reduced in suburban habitats where domestic cats achieve their highest densities. In contrast, if bottom-up processes drive variation in survival, we expect survivorship to show a quadratic relationship with peak survival at intermediate degrees of urbanization (increased food resources) and low survival at the two ends of the urbanization spectrum. To test these hypotheses we develop and compare a set of competing models of annual survivorship using various combinations of model covariates.

Methods

This study was conducted from 2000 to 2012 within a 100 km spatial extent encompassing a rural-to-urban land use gradient in the greater Washington D.C. and Baltimore, M.D. metropolitan region. Research in urban environments is often limited by accessibility and adequate coverage of the urban gradient (Cooper et al. 2007). To alleviate this problem we utilized sites (n =242) that were part of Neighborhood Nestwatch (hereafter referred to as "NN"), which is an ongoing citizen science project run by the Smithsonian Migratory Bird Center. NN is the ideal sampling framework for studying the effects of urbanization on avian demography because it provides access to residential properties within core urban and suburban environments as well as forested and agricultural land cover types (Figure 3.1). By incorporating privately owned land within our study design, we are able to capture portions of the urban and suburban matrix not normally monitored in

avian survivorship studies. To assess whether NN sites adequately represent the urbanization gradient within our study area we compared the proportional land cover within a 500-meter radius of sampled sites to randomly selected sites using a two-sample Kolmogorov-Smirnov test. These analyses showed that our sampled sites were largely representative of the distribution of land cover types typically used to characterize the rural-to-urban gradient (e.g., core urban, suburban, agricultural, and forested).

Annually, NN technicians visit participant properties during the avian breeding season (between the months of May and August, sites are predominantly visited by one technician). During each visit, technicians provide an educational banding demonstration for program participants and set two to eight mist nets for a period of three to five hours of mark-recapture. Birds are captured using target netting with playback of mobbing calls or conspecific song. Individuals are marked with a unique US Fish and Wildlife aluminum band and a unique combination of colored plastic bands. Technicians measure body mass (to the nearest 0.01 g) on an electronic balance and unflattened wing chord (to the nearest 0.25 mm) with a wing rule. Birds are aged into hatch year (HY) and after hatch year (AHY) age classes using plumage, skull ossification, or molt criteria (methodologies vary by species, see Pyle 1997). During the annual banding visit, technicians spend one hour attempting to resight birds banded during previous visits. We search all accessible areas within a 200 m radius of the site, using playback techniques. At the end of each visit, participants are provided with a list of color-banded birds, trained on resighting techniques, and expected to attempt to resight and report observations of marked individuals throughout the year.

Model Development

We estimated the annual survival of seven species of birds most common across the development gradient within our study region: American Robin (*Turdus migratorius*), Carolina

Chickadee (*Poecile carolinensis*), Carolina Wren (*Thryothorus ludovicianus*), Gray Catbird (*Dumetella carolinensis*), House Wren (*Troglodytes aedon*), Northern Cardinal (*Cardinalis cardinalis*), and Song Sparrow (*Melospiza melodia*). Species showed variation in capture rates along sampling gradient due to differences in abundance rather than limited sample size. We fit Cormack-Jolly-Seber survivorship models to these data to investigate the effects of individual covariates on apparent survivorship (Φ) and the probability of detecting marked individuals given that they remained within the sampling location (p). All models were constructed in the R package RMark (v. 2.14.1, R Core Team 2014, Laake 2013) and implemented in Program MARK (White and Burnham 1999). Covariates used in model construction were unstandardized and are described in detail below (also see Table 3.1). We used Akaike's Information Criteria (AIC, Akaike 1973) to select the best models among a set of biologically plausible candidate models (see below).

We used AIC_c and Akaike weights to identify the models best supported by the data. Models in which the ΔAIC_c between a given model and the best model was less than 2 were considered equally supported by the data (Burnham and Anderson 2002). We used normalized Akaike weights, the ratio of the likelihood of a given model relative to the sum of the likelihood across models, to evaluate the weight of evidence for a given model relative to the full set of candidate models. We further assessed the effects of predictor variables by averaging β estimates and unconditional standard errors by their AIC weights across candidate model set (Burnham and Anderson 2002).

To account for variation or potential bias in the estimates of detectability and survivorship, we constructed an *a priori* model for each species that included sex, time-since-marking, body condition, and project participant resight effort covariates. Because model selection and subsequent parameter estimates can become unstable (high variance) by over-fitting models (>10 parameters), especially when there is an insufficient sample size for an individual group variable (Breiman 1996, Burnham and Anderson 2002), we constrained our model set to those in which the parameter

estimates were identifiable (see Cooch and White 2013). Here are referring to extrinsic identifiability (*sensu* Cooch and White 2013), where parameter estimates are at or near their boundary (0 or 1) or are otherwise unidentifiable because of insufficient sample size. Ultimately, we excluded these "over-parametrized" models that contained more parameters than can be accommodated by the data (Laake, pers. comm.). Therefore not all covariates could be included in *a priori* models for each species (see Table 3.1).

Territorial males may be much more likely to be encountered than females due to behavioral differences (Amrhein et al. 2012), therfore *sex* was included as a binary dummy covariate for estimating detectability. Likewise, because males and females may experience differential rates of survival (Donald 2007) or site fidelity (Murphy 1996), sex was also used as a covariate for Φ to account for variation in survival or emigration.

A population of birds captured during a given sampling event could contain both transient and resident individuals. Because there is a low probability of reencountering transient birds, failure to account for this could negatively bias survival estimates (Pradel 1996). We incorporated transience in the model structure by including a binary time-since-marking (TSM) term for the estimation of Φ. We then calculated separate survival estimates for the year after the initial capture occasion and between the second and following years of sampling. Because males and females may show differential rates of transience (Murphy 1996), an interaction term between TSM and sex was included within the *a priori* model.

Body condition is a potentially important determinant of avian survivorship in different environments (Johnson et al. 2005) and is theorized to decline in urban environments (Shochat 2004). To incorporate the effects of body condition on Φ, we used a scaled body condition index (BCI) derived from body mass and wing chord lengths (Peig and Green 2009). Because variation in

body condition may have differential effects on the survival of males and females, we included an interaction term between sex and BCI within the *a priori* model.

While we acknowledge the potential of time-dependence in both survivorship and detection probabilities, models with both time and covariates had insufficient sample size to provide identifiable parameters (see above). However, to examine the potential for temporal variation in vital rates we ran simplified models in which survival was a function of time for all seven species. Of the seven species, only Carolina Wren showed significant differences in survival among years (χ^2 = 37.11, df = 10, P = 0.0001). A reduced model set for Carolina Wren with an impervious by year interaction received some support but was not the best-supported model. Due to funding and logistical constraints, neither resighting nor banding effort was consistent across years and several sites were not sampled during every year of the study or discontinued. To account for this, individual observations in the encounter history were coded as encounter occasions, occasions in which an individual was not encountered, and unsampled occasions ("1", "0", and ".", respectively). While this technique (dot notation) has been used to account for missing sampling data (e.g., Danner et al. *in press*), a drawback of this method is that goodness-of-fit tests are not currently available to estimate overdispersion (ĉ) with missing data.

We examined the influence of citizen scientist sampling in our study by comparing estimates of detectability using data gathered by citizen scientists versus those collected by NN technicians. Because both technicians and participants attempted to resight birds at several locations, we were unable to evaluate the origin of individual observations. To account for citizen scientist *participation*, we therefore separated encounter records into those that originated from sites that included participant data ("active" sites, n = 100) and those that did not ("inactive" sites, n = 140), coded as a binary dummy variable.

To assess the effect of urbanization on avian survival, we compared the *a priori* model for each species with models that included our urbanization metric, impervious surface (Table 1). We used the proportion of impervious surface (IMP) within a 500 m radius of NN sites to characterize the degree of urbanization at each banding location. This proxy variable and scale of analysis was chosen because they have been found to be most predictive of avian demographic response to urbanization (see Ryder et al. 2010). Moreover, impervious surface is often used to characterize the ecological effects of urbanization gradient because it reflects the variation in habitat distribution and quality across the rural-to-urban gradient (reviewed in McKinney 2002). Across our samples, impervious surface was highly predictive of core urban and suburban land cover types. At lower proportions of impervious surface, our study sites are predominantly comprised of agricultural or forested habitats.

We obtained 30 m resolution impervious surface data from the 2006 National Land Cover Database (Fry et al. 2011) and determined the mean impervious surface within a 500 m neighborhood of each map pixel using the raster package in R (Hijmans 2014). Because several NN sites adjacent to the Chesapeake Bay and Potomac River included open water within the 500 m radius, this land-use type was excluded from estimates of proportional impervious surface cover. Additionally, because avian response to urbanization may be nonlinear, we included a quadratic term for impervious surface (IMP2) as a model covariate for candidate models.

Results

A total of 4,379 individuals, captured from 242 NN sites, were used in this analysis (Figure 3.1, Table 3.2). Among these individuals, 79% were never reencountered (n = 3,462). Across species, the ΔAIC_c of the full *a priori* model relative to a null model with no covariates (ϕ~1, p~1) was 18.5, suggesting considerable support the inclusion of *a priori* variables. Detailed results on the impact of

citizen scientist participation on detection probability are presented in supplementary material (see Appendix B, Table B2, Figure B1). There was supportive evidence that survival and detection estimates varied markedly between males and females and by species (Figure 3.2). These estimates are reported across time-since marking classes. Sex-specific estimates of survival and detection were not identifiable for House Wren or Song Sparrow because of small sample sizes (see Figure 3.2). Models that included additional urbanization variables received some support for six of the seven species (Table 3.3).

There was strong model support for variation in annual survivorship along the rural-to-urban gradient for American Robin, Song Sparrow, Northern Cardinal, and Gray Catbird (Figure 3.3 and Table 3.4). Annual survival probabilities for American Robin and Song Sparrow were highest at intermediate levels of urbanization (45 and 47% impervious surface, respectively), with both species exhibiting a strong quadratic response to impervious surface (Figure 3.3, Table 3.4). Northern Cardinal and Gray Catbird exhibited a nearly linear increase in apparent survival with increasing urbanization. While there was substantial support for models that included a quadratic response to impervious surface cover for both of these species, estimates at the upper end of the rural-to-urban gradient contain considerable uncertainty due to small sample sizes at highly urban sites. In contrast, the *a priori* model and impervious surface models received equal support for Carolina and House Wren, with apparent annual survival decreasing with urbanization (Figure 3.3 and Table 3.4). However, no individuals of these species were reencountered at sites with greater than 50 % impervious surface and beta estimates contain considerable uncertainty (Table 3.4). There was no evidence that impervious surface was predictive of Carolina Chickadee survival.

Discussion

Understanding the demographic consequences of anthropogenic habitat change is essential as natural habitats are being rapidly converted to human dominated landscapes. While the proportion of urban land cover in the United States increased by 34% during the last two decades of the twentieth century, it is expected to increase by an additional 79% between 2000 and 2025 (Alig et al. 2004). Despite the increasing pace of urbanization, few studies have addressed survivorship of adult birds in urban environments (Chace and Walsh 2006) and none to our knowledge have yet explored survival along the rural-to-urban gradient from within urban or suburban matrices (but see Stracey and Robinson 2012). Here, we utilized a unique study designed to determine the effects of urbanization on the annual avian survival and test hypotheses about which processes (e.g., top-down vs. bottom up) regulate bird populations in human-dominated landscapes. We evaluated the annual survival of seven bird species common to suburban and urban matrices in a large-scale study of avian demography. By using the Smithsonian's Neighborhood Nestwatch program, which utilizes citizen scientists throughout the Washington D.C. greater metropolitan area to provide sampling locations and resight banded birds, we were able to identify variation in survivorship along the rural-to-urban gradient, with higher apparent survival in suburban and urban environments for four of our seven species than at the rural end of the gradient. Cumulatively, our results suggest that the effect of urbanization influences avian vital rates, but that the regulatory mechanisms may be species-specific.

Previous studies estimating adult survivorship of birds in human dominated systems have reported mixed results, most often showing little or no influence of urban land cover. Rodewald and Shustack (2008, 2008a), for example, found no difference between survivorship of Northern Cardinals occupying forests embedded within an urban matrix versus those occupying forests embedded within a rural matrix. In contrast, our results provide supportive evidence for differential

survival rates along the rural-to-urban gradient in six of our seven study species. Populations of these species often exhibit peak abundances in urban-suburban matrix (Blair et al. 1996). As such, the disparity between our results and those of other urban demographic studies may have resulted from differences in sampling design where we sampled extensively within the matrix as opposed to embedded forest parks. This suggests that the demographic effects of urbanization on matrix-dwelling species may be best observed from the urban-suburban matrix itself. These results underscore the potential importance of local habitat quality on avian demographic processes in human-dominated landscapes.

Top-down and bottom-up controls on avian population processes

Observed patterns of survival across the rural-to-urban gradient may offer clues as to mechanisms that underlie the demographic response. Urban environments are hypothesized to influence avian survival via increased rates of disease transmission, novel threats (e.g., collisions with man-made objects, Chace and Walsh 2006), and locally high densities of predators such as domestic and feral cats (Sorace 2002, but see Shochat et al. 2010). Therefore, if avian survival is determined by top-down controls, we expected that survivorship would decline with increasing urban land cover. Conversely, if resource availability determines survival in urban landscapes, it is expected that survivorship would be enhanced in these environments for many species due to anthropogenic resources (e.g., supplemental feeding), high densities of some invertebrates (especially for ground-foraging birds, see Szlavecz et al. 2006), and abundant fruit resources associated with ornamental and non-native plants (McIntyre 2000, Reichard et al. 2001, Craves 2009, but see Tallamy 2004 and Burghardt et al. 2009). The extent to which bottom-up effects regulate avian populations are likely dependent on the degree of urbanization, the type and abundance of available resources, and the life histories of the affected bird species.

Higher apparent survivorship for four of our focal species (American Robin, Gray Catbird, Northern Cardinal, and Song Sparrow) fits the pattern the expected of bottom-up controls on survival with increasing urbanization. These species are often considered habitat generalists (Poole 2013) and may therefore more readily adapt to challenges associated with urban landscapes (McKinney and Lockwood 1999). Additionally, a considerable proportion of the diets of these species consist of fruit and invertebrate resources (Poole 2013) many of which are more abundant in urban-suburban environments (Raupp et al. 2010). Availability of winter fruit resources on non-native and ornamental plants may provide relaxation from starvation pressures during winter months when survival of the resident species is dependent on a consistent food supply (Shochat et al. 2010). Because our support for the bottom-up control hypothesis is correlational, future studies that assess the distribution of resource availability are necessary.

Carolina Chickadee, Carolina Wren, and House Wren each exhibited their highest rates of survival at the rural portions of the gradient, with Carolina Chickadee showing no response to urbanization. The peak apparent survival of these species, however, was similar to the lowest annual survival of Northern Cardinal and Song Sparrow, suggesting low relative survival rates for these species across our study area. All of these cavity-nesting species exhibit very low abundances at the urban end of the gradient (Evans et al., unpublished data). A lack of these individuals within the suburban and urban portions of the matrix may reflect a reduction in nesting resources due to a loss of adequate cavity trees or interspecific competition for nest cavities with matrix-dwelling species such as the European Starling (*Sturnus vulgarus*) and House Sparrow (*Passer domesticus*; Newton 1994, Blewett and Marzluff 2005). Alternatively, observed patterns of survivorship and abundance for these species may be driven by declines in the size of suitable forest patches, the quality of the surrounding matrix along the rural-to-urban gradient, and/or behavioral avoidance of open urban habitats (Robbins et al. 1989, Medley et al. 1995).

Potential influence of urbanization on avian fitness

The influence of urbanization on adult survival may significantly alter avian fitness in human-dominated systems. Although the response of Northern Cardinal to urbanization was somewhat moderate, strong positive effects of urbanization on annual survival estimates of American Robin, Gray Catbird, and Song Sparrow suggest that habitat modification associated with urban land cover may positively influence population persistence for these species. If adult survivorship plays a dominant role in population persistence, our results predict differential population trajectories for Gray Catbird, Northern Cardinal, American Robin, and Song Sparrow relative to Carolina Wren, House Wren, and Carolina Chickadee in urban areas. While the inference of this study is limited to the greater Washington D.C. area and species common to this region, the NN model is currently being adopted in several other large metropolitan areas to provide a broader understanding of how urbanization shapes avian population demography (Marra unpubl. data).

Taken in concert with the finding that our study species exhibit greater nest success at higher levels of urbanization within the Washington, D.C. metropolitan area (Ryder et al. 2010), our results suggest that the suburban-urban matrix may be a source for American Robin, Gray Catbird, Northern Cardinal and Song Sparrow in this region. Populations of these species exhibited their lowest rates of adult survivorship and nest success within the rural habitats of our study area, suggesting that undeveloped portions of this landscape may actually constitute a demographic sink for these species (Pulliam 1988). Data from our study region on Gray Catbirds suggest the dynamics of these population processes are largely driven by post-fledging survival and recruitment in suburban habitat contexts (see Balogh et al. 2011). The vital rate data provided here is a crucial starting point for understanding source-sink dynamics of bird populations along the urbanization gradient.

Conclusion

The costs and benefits of urbanization may differentially affect avian vital rates; therefore our understanding of the demographic consequences and sensitivity of populations to extinction in urban environments is of paramount importance. Our findings that the adult survival of several of our focal species was higher in urban relative to rural environments, in conjunction with previous findings of higher rates of nest success (Ryder et al. 2010), suggest that the effects of urbanization on these life history stages may facilitate the expansion of populations of some species of urban-adapted birds. It is important to highlight that this study focused on a suite of species prevalent in the urban-suburban matrix. Our work cannot, therefore, assess the impact of urbanization on true urban-avoiding species, which have likely been disproportionately affected by anthropogenic habitat modification. Moreover, while the results of this study document substantial variation in apparent adult survival, even among urban-adapted species, our work cannot address how the mosaic of habitats within core urban and suburban environments shapes spatial and temporal population dynamics. Here we present correlative evidence of bottom-regulation for a suite a species, yet further study is necessary to directly assess how the distribution of risks, such as building collisions and free-roaming cats, and resources, such as fruit and arthropods, vary along the rural-to-urban gradient. Ultimately, fully understanding how urbanization shapes ecological and evolutionary processes and mitigating its effects will require comparative studies that jointly document the mechanisms and the life-history traits of both urban adapted and urban avoiding species.

TABLES

Table 3.1. Variables used in the development of *a priori* and urbanization-participation models. Continuous variables are reported in upper case and factors are reported in lower case.

Model set	Variable	Variable description	Parameter
a priori	BCI	Scaled body condition index	$\Phi^{a,b,c}$
a priori	sex	Binary sex (male, female)	$\Phi^{a,b}$, $p^{a,b,c}$
a priori	tsm	Binary time-since-marking	$\Phi^{a,b,c}$
a priori	sex:BCI	Interaction term between sex and body condition index	$\Phi^{a,b}$
a priori	sex:tsm	Interaction term between sex and time-since-marking	$\Phi^{a,b}$
a priori	part	Binary active vs. inactive participation by citizen-scientists	p^{a}
urbanization	IMP	Impervious surface cover (%)	$\Phi^{a,b,c}$
urbanization	IMP2	Impervious surface, quadratic form	$\Phi^{a,b,c}$
urbanization	IMP:sex	Interaction term between impervious surface and sex	$\Phi^{a,b,c}$

a) *a priori* model for AMRO, CACH, GRCA, NOCA: ϕ (sex+BCI+tsm+sex:BCI+sex:tsm), p (sex+ part)
b) *a priori* model for CARW: ϕ (sex+BCI+tsm+sex:BCI+sex:tsm), p (sex)
c) *a priori* model for SOSP and HOWR: ϕ (BCI+tsm), p (sex+ part)

Table 3.2. Sample counts of captured and reencountered birds in the Neighborhood Nestwatch program across years.

Species	ALPHA	Female captures	Male captures	Total captures	Female recaptures	Male recaptures	Total recaptures
American Robin	AMRO	198	218	**416**	24	22	**46**
Carolina Chickadee	CACH	192	211	**403**	43	57	**100**
Carolina Wren	CARW	211	251	**462**	37	74	**111**
Gray Catbird	GRCA	329	646	**975**	38	143	**181**
House Wren	HOWR	191	432	**623**	15	49	**64**
Northern Cardinal	NOCA	402	603	**1005**	85	186	**271**
Song Sparrow	SOSP	101	407	**508**	21	131	**152**
Totals across species		1624	2768	**4392**	263	662	**925**

Table 3.3. Summary statistics of the candidate model set examining the impact of urbanization on avian survival within the greater Washington, DC area. Models are ranked from best to worst fit based on AIC_c. The *a priori* model sets are described in Table 3.1.

Species	Model	k	AIC_c	ΔAIC_c	*w*	-2LogLik
AMRO	ϕ(*a priori* + IMP + IMP^2), *p*(sex + part)	11	3184.48	0	0.721	3161.91
	ϕ(*a priori* + IMP + IMP^2 + IMP:sex), *p*(sex + part)	12	3186.58	2.10	0.252	3161.91
	ϕ(*a priori* + IMP), *p*(sex + part)	10	3191.79	7.30	0.018	3171.32
	ϕ(*a priori* + IMP + IMP:sex), *p*(sex + part)	11	3193.83	9.34	0.006	3171.26
	ϕ(*a priori*), *p*(sex + part)	9	3198.41	13.92	0	3180.02
CACH	ϕ(*a priori*), *p*(sex + part)	9	16215.66	0	0.479	16197.33
	ϕ(*a priori* + IMP), *p*(sex + part)	10	16217.73	2.07	0.169	16197.32
	ϕ(*a priori* + IMP + IMP:sex), *p*(sex + part)	11	16217.75	2.08	0.168	16195.25
	ϕ(*a priori* + IMP + IMP^2 + IMP:sex), *p*(sex + part)	12	16218.81	3.15	0.099	16194.22
	ϕ(*a priori* + IMP + IMP^2), *p*(sex + part)	11	16219.16	3.49	0.083	16196.66
CARW	ϕ(*a priori*), *p*(sex)	8	17657.64	0	0.498	17641.40
	ϕ(*a priori* + IMP), *p*(sex)	9	17659.54	1.90	0.192	17641.24
	ϕ(*a priori* + IMP + IMP:sex), *p*(sex)	10	17660.44	2.80	0.122	17640.08
	ϕ(*a priori* + IMP + IMP^2), *p*(sex)	10	17660.83	3.18	0.101	17640.46
	ϕ(*a priori* + IMP + IMP^2+ imp:sex), *p*(sex)	11	17661.17	3.52	0.085	17638.73
GRCA	ϕ(*a priori* + IMP + IMP^2 + imp:sex), *p*(sex + part)	12	9814.62	0	0.442	9790.37
	ϕ(*a priori* + IMP + IMP:sex), *p*(sex + part)	11	9815.99	1.36	0.223	9793.77
	ϕ(*a priori* + IMP + IMP^2), *p*(sex + part)	11	9816.52	1.90	0.170	9794.31
	ϕ(*a priori* + IMP), *p*(sex + part)	10	9816.69	2.06	0.157	9796.51
	ϕ(*a priori*), *p*(sex + part)	9	9823.14	8.51	0.006	9804.99
HOWR	ϕ(*a priori*), *p*(sex + part)	6	6181.53	0	0.446	6169.42
	ϕ(*a priori* + IMP + IMP^2), *p*(sex + part)	8	6181.85	0.31	0.381	6165.65
	ϕ(*a priori* + IMP), *p*(sex + part)	7	6183.44	1.90	0.172	6169.23
NOCA	ϕ(*a priori* + IMP), *p*(sex + part)	10	41351.09	0	0.440	41330.94
	ϕ(*a priori* + IMP + IMP^2), *p*(sex + part)	11	41352.19	1.09	0.254	41330.01
	ϕ(*a priori* + IMP + IMP:sex), *p*(sex + part)	11	41353.13	2.03	0.159	41330.94
	ϕ(*a priori* + IMP + IMP^2 + IMP:sex), *p*(sex + part)	12	41354.20	3.10	0.093	41329.98
	ϕ(*a priori*), *p*(sex + part)	9	41355.34	4.24	0.052	41337.21
SOSP	ϕ(*a priori* + IMP + IMP^2), *p*(sex + part)	8	19245.18	0	0.870	19228.98
	ϕ(*a priori* + IMP), *p*(sex + part)	7	19249.14	3.96	0.120	19234.99
	ϕ(*a priori*), *p*(sex + part)	6	19254.31	9.13	0.009	19242.20

Table 3.4. Model-averaged Beta estimates for the influence of the proportional cover of impervious surface on annual survival probability.

	Impervious surface (%)		Impervious surface^2	
Species	$\bar{\beta}$	$\overline{SE}$	$\bar{\beta}$	$\overline{SE}$
AMRO	11.78	3.04	-13.31	4.58
CACH	0.54	1.50	-3.88	5.31
CARW	-0.39	1.53	-4.31	7.05
GRCA	2.50	0.97	-3.21	2.20
HOWR	4.26	2.82	-16.42	10.51
NOCA	1.57	0.74	-2.01	2.06
SOSP	5.21	1.65	-6.38	2.59

FIGURES

Figure 3.1. The urbanization gradient as characterized by impervious surface and sampling sites (n =242) of the Neighborhood Nestwatch Program in greater Washington, DC, which formed the framework for the demographic analyses. Inset displays the general study region within the continental US.

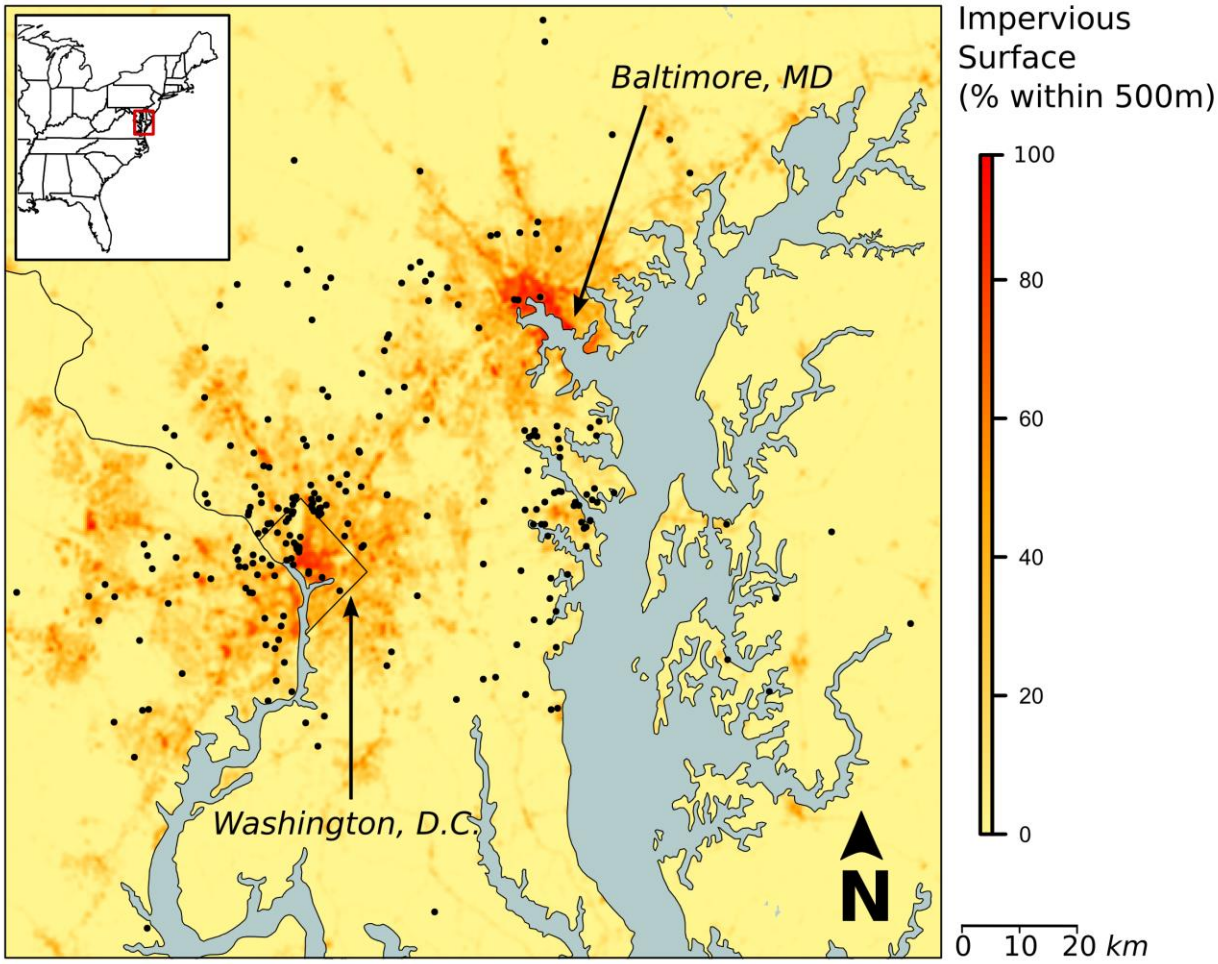
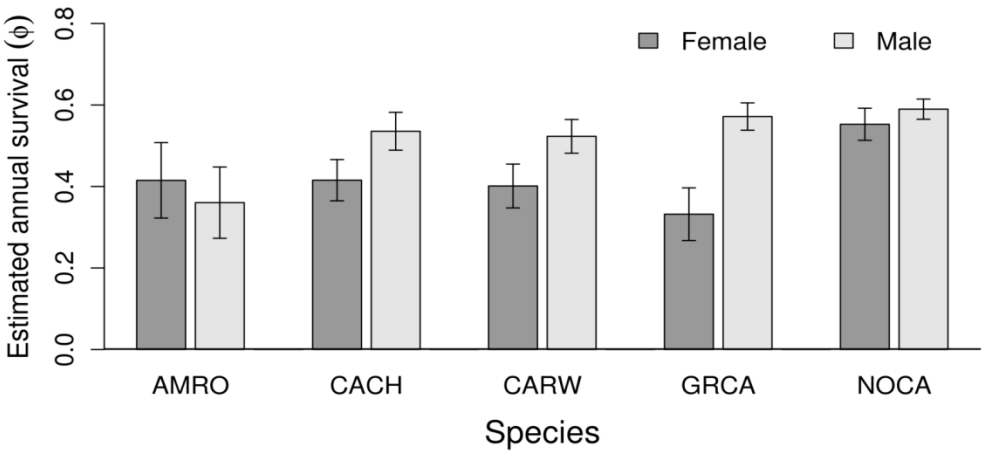


Figure 3.2. Estimates of A) annual survival and B) detection by species and sex along an urbanization gradient in greater Washington, DC. For species denoted with an asterisk (i.e., House Wren and Song Sparrow) did not have sufficient sample size to model the influence of sex on survival.



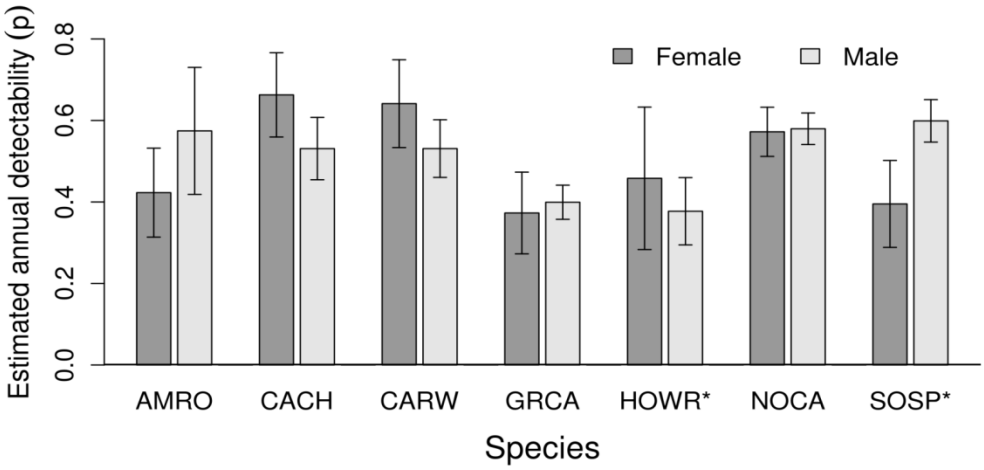
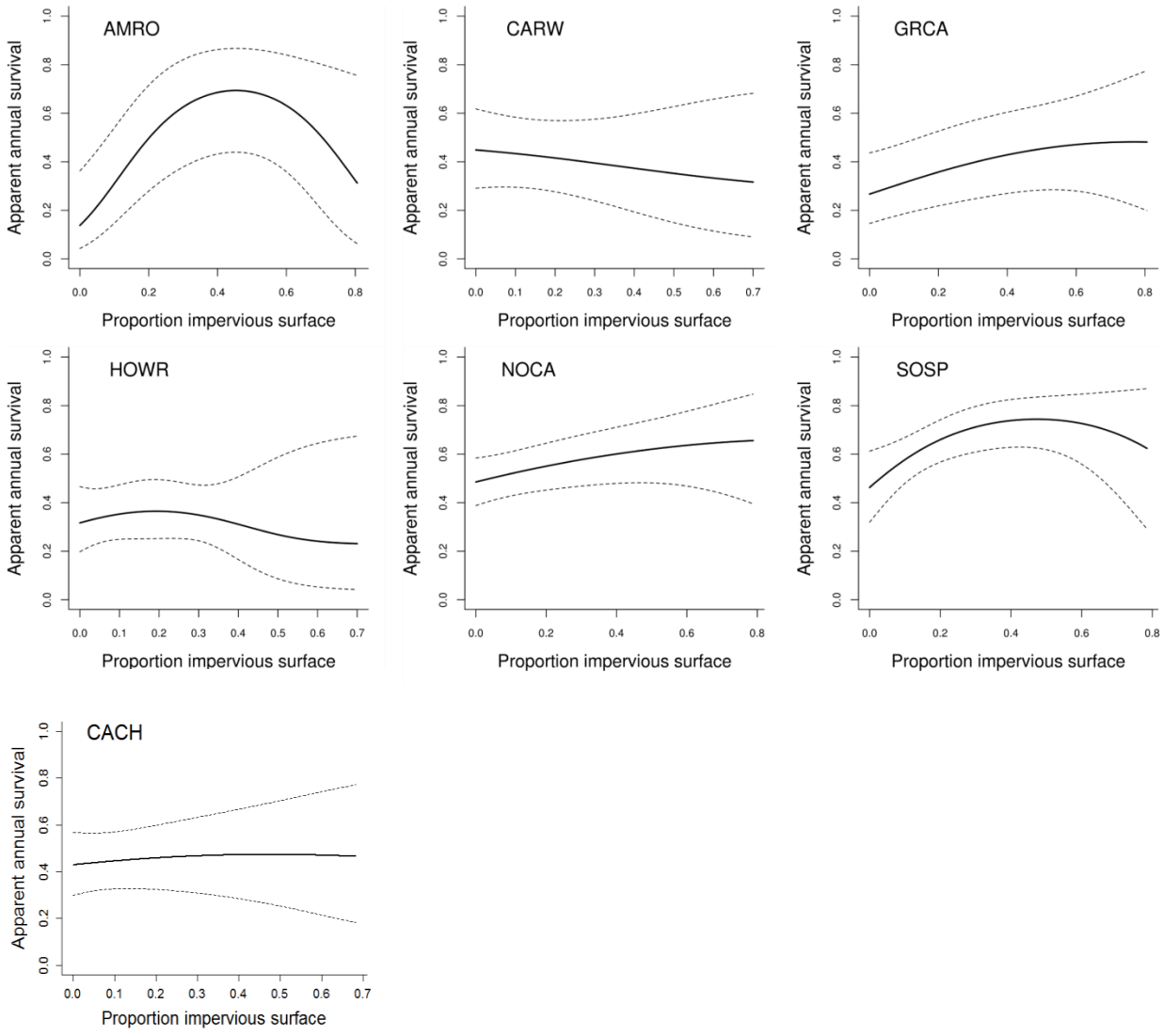


Figure 3.3. Model-averaged estimates of American Robin, Gray Catbird, Song Sparrow, and Northern Cardinal annual survival probabilities across the rural-to-urban gradient in greater Washington, DC.



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CHAPTER 4: CONCLUSIONS AND SYNTHESIS

Within this dissertation, I applied novel methodologies to address the biological response of birds to urban environments. The primary goal of this process was to determine how bird communities and populations are shaped by urbanization and thus provide an initial framework of key biological measures of avian response to the rural-to-urban gradient. In doing so, we addressed the environmental filtering of avian communities, spatial dispersal patterns in birds within the urban matrix, and adult survival of birds common to the rural-to-urban gradient in the eastern United States. As the amount of urban land cover is expected to triple in the first 30 years of this century (Seto 2012), and fate of wildlife in urban habitats remains a critical "frontier" in ecology (Picket et al. 2001), this research represents an important advancement in our knowledge of how urban ecosystems work.

Throughout biogeographic regions, the number of bird species in local communities has been shown to consistently decrease with urban land cover (McKinney 2006). While previous studies have used this and the response of individual guilds as evidence for environmental filtering (e.g., Croci et al. 2008), environmental filtering had not yet directly been examined and conflicting responses among guilds and regions have limited our ability to detect filtering processes. In Chapter 1, I found that the representation of life-history guilds in local species pools, i.e., functional diversity, was largely a non-random subset of the regional species pool – providing direct evidence for filtering – and the strength of filtering increased with increasing urban land cover. I further explored this pattern in diversity by examining the overall response of guilds to urban land cover in regards to the

abundance and relative abundance of representative species within local communities. While my observations largely fit expected patterns of relative abundance (e.g., a decline in insectivores across the rural-to-urban gradient, Blair and Johnson 2008), the influence of urban land cover on abundance provided unexpected results, as no guilds were shown to be positively associated with urban land cover, despite expectations that birds with generalist traits, such as omnivores (e.g, Jokimaki et al. 2014) have an advantage in urban environments. Therefore, observed increases in the proportional abundances of these guilds in this and previous studies (e.g., Blair and Johnson 2008) are likely driven by differential rates in decline among guilds. If this pattern is consistent across biogeographic regions, this requires us to rethink how we expect avian communities to respond to urbanization, as this result calls into question whether urban-adapted and exploiting species, often considered to be the "winners" of the urbanization process (McKinney and Lockwood 1999), simply "lose less" than urban-avoiding species.

Contrary to the suggestion that there are no "winners" to urbanization, in Chapter 3 we found no negative influence of urban land cover on survival – rather, for four of seven focal species, each of which are considered to be urban-adapted, survival was highest in suburban (two species) and urban habitats (two species). Among the remaining species, all of which are cavity-nesters and often considered to be urban-avoiding species, there was no observable impact of urbanization. While other studies have addressed the survival of birds in forested patches embedded within the urban matrix (e.g., Rodewald and Shustack 2008), this was the first study to examine survival from within the urban matrix and the only study to date to find an influence of urban land cover on adult survival. Our results coincide with the findings of Ryder et al. (2010), who found that nest success was higher in urban environments for our target species and study area. Despite our findings in Chapter 1 that these species exhibited lower abundance in urban relative to rural habitats, adult and

nestling survival estimates provide evidence that urban habitats may be a boon for populations of birds that are able to persist within the urban matrix.

The observed survival patterns in Chapter 3 fit our hypothesis that survival will be positively influenced by enhanced resources for some species in suburban and urban habitats. Urban environments are expected to confer increased mortality pressures associated with novel predators (Balogh et al. 2011), collisions (Chace and Walsh 2006), disease transmission (Kilpatrick 2011), and pollution loads (Roux and Marra 2007), and thus it would be expected that if direct, "top-down", processes determine survival then survival should decline across the rural-to-urban gradient. Conversely, with the exception of leaf-gleaning insectivores, for which there is a decline in prey abundance in many human-built habitats (Tallamy 2004), we speculate that our findings represent the enhancement of resources in urban environments, due to supplemental feeding (Doherty and Grubb 2002), increased ground arthropod densities (e.g., Szlavecz et al. 2006), and high abundances of non-native fruits in urban environments (e.g., McCusker et al. 2010). As the mechanisms that are expected to drive survival are often conflicting and context dependent, further research is necessary to determine which habitat features enhance or diminish avian population processes. In doing so, a shift in focus is necessary, from trends in vital rates associated with neighborhood-level habitats, as this study has addressed, to those associated with local-scale habitat features and individual mechanisms.

While Chapters 1 and 3 address the proportional urban land cover surrounding sites, in Chapter 2 we assessed the influence of habitat features and distribution between sites. Here, we evaluated the influence of land cover on dispersal – a key biological process that greatly affects avian community composition and population persistence. Despite its importance, dispersal has received

little attention in the study of the urban ecology of birds. Indeed, while several studies have shown movement to be influenced by the intensity of human development (e.g., Kennedy and Marra 2010), the fate of dispersers in urban environment remains largely unknown. To address this, we evaluated the spatial distribution of previously banded individuals (at least one year prior) in the landscapes surrounding banding stations. We found supportive evidence that the permeability of the landscape is a likely determinant of the dispersal patterns of two of four focal species. Because dispersal is critical to the persistence of metapopulations by linking local populations (e.g., Beier and Noss 1998), the influence of landscape permeability in the urban matrix is of key conservation concern. While our findings suggest that the distribution and quality of habitat between breeding locations influences dispersal processes, further exploration of the role of local-scale habitat features in determining the emigration, movement, and immigration decisions of birds is necessary.

Taken cumulatively, this dissertation provides strong evidence that urbanization influences key biological processes, including the composition of bird communities, the survival of birds, and the dispersal of birds across the rural-to-urban gradient. Addressing the influence of individual habitat features and mechanisms that shape each of the described patterns is crucial to determining how best to manage urban habitats for the maintenance of wildlife communities and populations. The findings herein offer a significant step forward in assessing the urban ecology of birds and thus provide a baseline with which to address avian conservation. As urbanization was the second leading cause of species endangerment in the 20th century and is expected to become the leading cause in the 21st century (Marzluff 2001), better understanding how to manage these environments is critical to minimizing its impacts.

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